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Ecological Risk Assessment of Recreational Boating as a Pathway for the Secondary Spread of Aquatic Invasive Species in the Great Lakes Basin

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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TABLE OF CONTENTS

ABSTRACT iv

RÉSUMÉ v

INTRODUCTION 1

SCOPE OF RISK ASSESSMENT AND OVERVIEW OF MODEL-BASED APPROACH 5

KEY ASSUMPTIONS OF MODEL-BASED APPROACH 7

ESTIMATING PROPAGULE PRESSURE FROM RECREATIONAL BOATING IN THE GLB 8

CHARACTERISTICS OF RECREATIONAL BOATING IN THE GLB 8

ESTIMATING THE FREQUENCY AND SPATIAL DISTRIBUTION OF RECREATIONAL BOATING IN THE GLB 12

FUNCTIONAL GROUPS OF AIS LIKELY TO BE TRANSPORTED BY RECREATIONAL BOATS IN FRESHWATER ECOSYSTEMS 17

PROBABILITY OF AIS SURVIVAL AND ESTABLISHMENT FOLLOWING BOATER-MEDIATED SECONDARY SPREAD IN THE GLB 22

RELATIONSHIP BETWEEN PROPAGULE PRESSURE AND ESTABLISHMENT 22

ESTIMATING THE OVERALL RATE OF BOATER-MEDIATED AIS SPREAD 24

OVERALL ESTIMATE OF THE ECOLOGICAL RISK OF RECREATIONAL BOATING AS A PATHWAY FOR THE SECONDARY SPREAD OF AIS IN THE GLB 32

CONCLUSIONS AND FINAL CONSIDERATIONS 52

REFERENCES CITED 54

APPENDIX 1.0 QUESTIONNAIRE TO DOCUMENT RECREATIONAL BOATING IN THE GLB 58

APPENDIX 2.0 MODEL PARAMETERS AND DEMOGRAPHIC CHARACTERISTICS 69

APPENDIX 3.0 TIMELINES OF SECONDARY SPREAD DUE TO RECREATIONAL BOATING 70

PHYTOPLANKTON FUNCTIONAL GROUP 70

PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP 72

NON-PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP (HIGH INVASIVENESS) 74

NON-PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP (MODERATE INVASIVENESS) 76

MOLLUSC FUNCTIONAL GROUP (HIGH INVASIVENESS) 78

MOLLUSC FUNCTIONAL GROUP (MODERATE INVASIVENESS) 80

MACROPHYTE FUNCTIONAL GROUP 82

NON-PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP (HIGH INVASIVENESS) FOLLOWING A 25% REDUCTION IN MODEL PARAMETERS 84

ABSTRACT

A model-based assessment was conducted to estimate the ecological risk of recreational boating as a pathway for the secondary spread of aquatic invasive species (AIS) in the Great Lakes basin (GLB). Boater-mediated spread was quantified based on the number, type, and spatial distribution of recreational boating trips in the GLB, the infestation of boats with functional groups of fouling AIS (plankton, molluscs, and aquatic macrophytes), and the likelihood that organisms would establish reproducing populations based on demographic factors and transported population sizes. Boater-mediated spread timelines were estimated probabilistically up to a maximum period of ten years, allowing the expected timeline of spread to be compared with baseline estimates of natural dispersal. The model revealed a total of 11.8 M yearly recreational boating events in the GLB (3.8 M originating at Canadian recreational access sites, 8.0 M originating at U.S. recreational access sites). The large number of boating events, combined with relatively high densities of transported organisms, was sufficient to overcome demographic constraints to establishment in many cases. Boater-mediated spread varied across functional groups and was fastest for invasive phytoplankton, with among-lake spread expected in as little as a single year in some scenarios. A relatively robust spatial pattern emerged with the highest rate of spread between neighbouring lakes; however, upstream movement through GLB lock structures and among multiple lake basins was possible with sufficient time (e.g., average modeled estimate of eight years for invasive phytoplankton to spread from the St. Lawrence River to Lake Superior). Two ecological consequences emerged. Boating activity was mostly unlikely to surpass downstream rates of natural dispersal, though in some cases could be exceeded by a period of up to four years. However, for all functional groups of AIS, boating activity was far more likely to lead to new upstream pathways of secondary spread that would otherwise be unlikely to occur through natural dispersal at short timescales (10–20 years). The overall risk of secondary spread was highest for Lake Superior due to the frequent development of upstream pathways. Risk was usually moderate for Lake Michigan, Lake Huron, and Lake Erie, while risk was generally low for Lake Ontario and the St. Lawrence River because boater-mediated rates of spread were consistent with expectations under natural dispersal. Results were sensitive to background estimates of natural dispersal, indicating that the risk of secondary spread would be higher if natural dispersal progressed more slowly than expected. These findings indicate that for certain geographic routes and most functional groups of AIS, increased attention to in-water recreational boating as a pathway of the secondary spread of AIS is warranted.

Évaluation des risques écologiques associés à la navigation de plaisance comme voie de propagation secondaire d'espèces aquatiques envahissantes dans le bassin des Grands Lacs

RÉSUMÉ

Une évaluation fondée sur des modèles a été réalisée pour estimer les risques écologiques associés à la navigation de plaisance comme voie de propagation secondaire d'espèces aquatiques envahissantes (EAE) dans le bassin des Grands Lacs. La propagation par les bateaux de plaisance a été quantifiée à partir du nombre, du type et de la répartition spatiale des sorties de plaisance dans le bassin des Grands Lacs, de l'infestation des bateaux par des groupes fonctionnels d'EAE encrassantes (plancton, mollusques et macrophytes aquatiques), et de la probabilité que les organismes établissent des populations reproductrices en fonction des facteurs démographiques et de la taille des populations transportées. Les calendriers de propagation par bateau ont été estimés de façon probabiliste jusqu'à une période maximale de dix ans, permettant ainsi de comparer l'échéancier prévu de la propagation aux estimations de référence de la dispersion naturelle. Le modèle a révélé un total de 11,8 millions de sorties de bateaux de plaisance par année dans le bassin des Grands Lacs (3,8 millions proviennent de points d'accès de plaisance canadiens et 8 millions de points d'accès américains). Ce grand nombre de sorties, combiné aux densités relativement élevées des organismes transportés, était suffisant pour surmonter les contraintes démographiques associées à l'établissement dans de nombreux cas. La propagation par bateau variait selon les groupes fonctionnels et était plus rapide pour les espèces envahissantes de phytoplancton, dont la propagation entre les lacs pouvait se produire en une seule année dans certains scénarios. Un profil spatial relativement fiable a été obtenu, le taux de propagation étant le plus élevé entre des lacs voisins; toutefois, le déplacement en amont, en franchissant les écluses du bassin des Grands Lacs et entre plusieurs bassins, était possible si le temps était suffisant (p. ex., estimation modélisée moyenne de huit ans pour la propagation d'espèces envahissantes de phytoplancton du fleuve Saint-Laurent jusqu'au lac Supérieur). Deux conséquences écologiques sont apparues. Les activités de plaisance étaient généralement peu susceptibles de dépasser les taux de dispersion naturelle en aval, bien que dans certains cas, ce soit possible, et ce, d'une période pouvant aller jusqu'à quatre ans. Cependant, pour tous les groupes fonctionnels d'EAE, les activités de plaisance étaient beaucoup plus susceptibles d'ouvrir de nouvelles voies de propagation secondaire vers l'amont qui, autrement, auraient peu de chances de se produire par dispersion naturelle à court terme (10 à 20 ans). C'est dans le lac Supérieur que le risque global de propagation secondaire a été estimé le plus élevé, en raison de la création fréquente de voies de propagation vers l'amont. Les risques étaient réputés moyens pour le lac Michigan, le lac Huron et le lac Érié et en général faibles pour le lac Ontario et le fleuve Saint-Laurent, parce que les taux de propagation par bateau étaient proches des taux de dispersion naturelle prévus. Les résultats étaient sensibles aux estimations de base de la dispersion naturelle, ce qui indique que le risque de propagation secondaire serait plus élevé si la dispersion naturelle progressait plus lentement que prévu. Selon ces constatations, pour certaines voies géographiques et la plupart des groupes fonctionnels d'EAE, il convient donc de s'intéresser davantage à la navigation de plaisance à titre de voie de propagation secondaire d'EAE.

INTRODUCTION

Aquatic invasive species (AIS) cause profound ecological changes within freshwater systems, with impacts characterized by altered food webs (Vander Zanden et al. 1999), increased competition and predation (Jackson and Mandrak 2002), loss of native species (Sala et al. 2000; Rahel 2007), and reduced genetic variability (Phillip 1991; Echelle and Echelle 1997). As a result of these ecological impacts, AIS also disrupt ecosystem services and pose strong socioeconomic consequences (Pimentel et al. 2005; Colautti et al. 2006; Drake and Mandrak 2014a); therefore, understanding the ecological risk of AIS, including their mechanisms of introduction and spread, remains a research priority.

Because prevention management, i.e., managing invasions by preventing the introduction of known or suspected invaders, continues to be the most effective strategy for reducing future impacts, gaining a better understanding the ecological risk posed by AIS pathways within Canada is critical for developing integrated AIS risk management programs. Canada has numerous pathways known or suspected of introducing and spreading AIS that range in geographic distribution, spatial scale, and taxa. Common pathways for aquatic species include the water garden pathway (Marson et al. 2009a), the aquarium pathway (Marson et al. 2009b), the live food pathway, the live bait pathway (Drake and Mandrak 2014b, Drake and Mandrak 2014b, c), and the ballast water pathway (Casas-Monroy et al. 2014, 2015). A poorly understood pathway for the spread of AIS in freshwater ecosystems involves the recreational use of small boats. Most research of the ecological risk posed by small boats in freshwaters has focused on the probability of among-lake (i.e., overland) transport of AIS given the ability of certain AIS to foul boat and trailer surfaces (Jacobs and MacIsaac 2007, 2009; Rothlisberger et al. 2010), survive overland movement (Jerde et al. 2012), and become established in new localities following boater-mediated introductions (Bossenbroek et al. 2001; Leung et al. 2006; Muirhead and MacIsaac 2005, 2011). Comparatively little research has focused on how recreational boating activity can spread AIS within freshwater ecosystems as a function of on-water boating operations (but see Kelly et al. 2013).

Quantifying the ecological risk of recreational boating in Canada has become a research priority in response to several prominent inland lake invasions believed to be facilitated by the overland movement of recreational boats (e.g., Zebra Mussel and Quagga Mussel (*Dreissenid* spp.) invasions in central and western provinces, Spiny Waterflea (*Bythotrephes longimanus*), Fishhook Waterflea (*Cercopagis pengoi*), and Eurasian Watermilfoil (*Myriophyllum spicatum*) invasions in central provinces). Due to ongoing ecological impacts from boater-mediated AIS spread, a literature review of among-lake (i.e., overland) AIS introduction and spread resulting from recreational boating has been undertaken in a separate Canadian Science Advisory Secretariat (CSAS) Research Document (Drake 2017). However, the ability of trailered recreational boats to facilitate invasions among inland lakes as a result of fouled overland movements (e.g., Bossenbroek et al. 2001, MacIsaac et al. 2004, Muirhead and MacIsaac 2011, Rothlisberger et al. 2010) suggests that recreational boats may also facilitate the spread of AIS within and *between* large individual lakes and their connecting waters due to fouling and movement within the operational waterbody. The ecological risk associated with this pathway is currently unknown, but represents a potentially important mechanism of AIS spread within Canada's large freshwater ecosystems. The objective of this CSAS Research Document is to quantify the ecological risk associated with the secondary spread of AIS within large freshwater ecosystems in Canada, focusing primarily on the Laurentian GLB.

Ecological risk assessments of AIS undertaken by Fisheries and Oceans Canada (DFO) have been conducted using species- or pathway- based approaches. DFO's Center of Expertise for Aquatic Risk Assessment (CEARA) has developed guidelines for conducting species-based risk

assessments (Mandrak et al. 2012), which involve quantifying the probability of introducing a species (the joint arrival, survival, establishment, and spread) and the associated magnitude of ecological impacts (e.g., food web change; see Cudmore et al. 2012 for examples). Numerous species-based risk assessments have been completed by DFO, providing guidance about the likelihood of introducing species, the expected magnitude of impact, and the level of certainty associated with each step of the risk estimation. However, compared to species-based assessments, pathway-based assessments have been undertaken less frequently and lack equivalent methodological guidelines in Canada. Pathways of AIS introduction and spread vary in terms of the nature of introductions (e.g., primary introductions to Canada vs secondary spread within Canada) and the degree to which species are purposefully vs unintentionally transported (e.g., aquaculture vs ballast); therefore, different pathway-based risk assessment approaches may be appropriate depending on the nature of the pathway. For example, certain pathways may involve a defined set of transported species, such as the fishes or aquatic plants imported routinely for international trade, where the set of species may form the unit of observation (e.g., Gantz et al. 2014). In other cases, pathways may involve stochastic processes that introduce a diverse and rapidly changing variety of species, thereby favouring a more species-neutral approach combined with proxies of survival and establishment (e.g., Casas-Monroy et al. 2014, 2015).

Ecological concerns about the boater-mediated spread of AIS within large freshwater lakes in Canada are relevant when AIS have been introduced to a given water body through a primary or secondary mechanism (e.g., introductions via ballast water, baitfish activity, water gardens, natural dispersal, or among-lake recreational boating), and spread throughout the waterbody may be caused by recreational boating. Therefore, the pathway is essentially a mechanism for secondary spread at the scale of navigable waters. Should the boater-mediated spread of AIS within the waterbody be faster than the rate of spread and establishment expected under natural dispersal, ecological risk attributed to recreational boating would exist due to the increased rate at which ecological (and potentially, socio-economic) consequences of transported AIS are realized.

Given the conditional nature of this pathway, there are multiple scenarios where within-lake spread of AIS may pose relatively minor ecological consequences. For example, due to dispersal distances, small waterbodies (e.g., < 1000 ha) likely experience relatively rapid colonization of AIS across suitable habitat, suggesting that recreational boating would, in most instances, have little impact on the extent and rate of AIS dispersal in those systems. On the other hand, for the largest freshwater ecosystems in Canada (e.g., the Laurentian Great Lakes, Lake Winnipeg and Lake Winnipegosis, Great Bear and Great Slave Lake, and Lake Athabasca), the colonization of AIS across suitable habitat through natural dispersal may take substantial time (i.e., years) due to the large geographic distances required for natural dispersal to occur. While the rate of natural dispersal will ultimately be species dependent, boater-mediated movement within large lakes could substantially decrease the overall time required for AIS to spread across suitable habitat, thus increasing the rate at which AIS-derived ecological impacts occur. Large freshwater lakes often have directional flows and connecting channels that make it unlikely for certain species or life stages to disperse in an upstream direction, so it is also conceivable that boater activity could lead to the development of new pathways of AIS spread within boater-connected freshwater ecosystems. Studies from marine systems indicate that the boater-mediated spread of tunicates, kelp, and other fouling species can lead to new pathways of dispersal against prevailing water currents (Hunt et al. 2009, L. Chadderton, The Nature Conservancy, pers. comm), emphasizing the importance of investigating on-water recreational boating as a mechanism for facilitated upstream movements of AIS in large freshwater ecosystems.

The potential for recreational boating to introduce and spread invasive species within large freshwater lake ecosystems is a key uncertainty relating to AIS management in Canada. Given that this issue has received attention predominantly from a commercial vessel standpoint through the estimation of ballast-mediated AIS movements in the Laurentian Great Lakes (i.e., the Laker fleet: Casas-Monroy et al. 2014, 2015; Drake et al. 2015a, b), it is also necessary to contrast the relative role of recreational and commercial activity in facilitating secondary spread. The goal of this document is to assess the ecological risk posed by recreational boater-mediated AIS introduction and spread, focusing on the Laurentian GLB given substantial recreational boating activity (U.S. Army Corps of Engineers 2008; Rothlisberger et al. 2010) and prominent invasion history in the region.

Quantifying the ecological risk of recreational boating in the GLB is a function of the probability that boater activity will surpass (quicken) rates of natural dispersal of AIS, the consequence (magnitude) of faster spread attributed to boating, plus uncertainty inherent in the model-based assessment. In this risk assessment, likelihood categories were derived from Mandrak et al. (2012) (Table 1) and consequence categories were developed to assess the magnitude of boater-mediated secondary spread relative to natural dispersal (Table 2). By quantifying the probability of each consequence category occurring, risk distributions describe the likelihood of each spread consequence as a function of current projections of recreational boating activity in the GLB. An example of a hypothetical boater-mediated risk distribution is given in Figure 1. The vertical axis represents the probability (likelihood) that each consequence category (horizontal axis) will occur as a result of boater-mediated AIS spread. Certainty categories were derived to understand how deviations in model parameters would change the overall risk estimate (Table 3).

Table 1. Likelihood values as probability categories. Taken from Mandrak et al. 2012.

Likelihood	Probability Category
Very Unlikely	0.0–0.05
Low	>0.05–0.40
Moderate	>0.40–0.60
High	>0.60–0.95
Very Likely	>0.95–1.0

Table 2. Categories used to describe the consequence of secondary spread associated with recreational boating in the Great Lakes basin.

Generic Category	Change (Reduction) in Spread Timeline Attributed to Recreational Boating Compared with Natural Dispersal as Baseline
Very Low	No Change Relative to Natural Dispersal, or Reduction of < 1 Year Attributed to Recreational Boating
Low	Reduction of 1–2 Years Attributed to Recreational Boating
Moderate	Reduction of 3–4 Years Attributed to Recreational Boating
High	Reduction of 5 Years Attributed to Recreational Boating
Very High	Reduction of More Than 5 Years Attributed to Recreational Boating. The 'Very High' category defines the development of new upstream pathways where natural dispersal would be extremely unlikely to occur over a short (10–20 year) period for the sessile functional groups of organisms in this assessment.

Table 3. Certainty categories used to describe the sensitivity of the overall risk ranking to changes in model parameters.

Certainty Category	Description
Very Low Certainty	25% Change in Parameter Values Lead to Four Deviations in Modal Consequence Class (e.g., from Very High Consequence to Very Low Consequence)
Low Certainty	25% Change in Parameter Values Lead to Three Deviations in Modal Consequence Class (e.g., from Very High Consequence to Low Consequence)
Moderate Certainty	25% Change in Parameter Values Lead to Two Deviations in Modal Consequence Class (e.g., from Very High Consequence to Moderate Consequence)
High Certainty	25% Change in Parameter Values Lead to One Deviation in Modal Consequence Class (e.g., from Very High Consequence to High Consequence)
Very High Certainty	25% Change in Parameter Values Lead to No Change in Modal Consequence Class

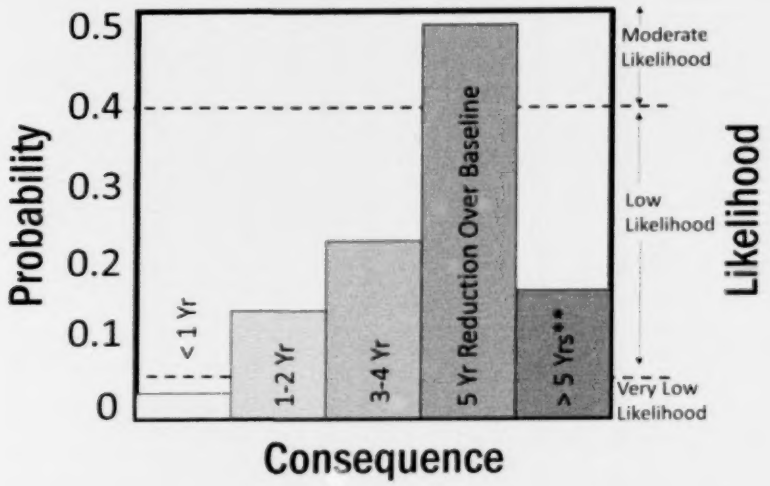


Figure 1. Hypothetical risk distribution of the secondary spread of AIS attributed to recreational boating in the Great Lakes basin. Likelihood (synonymous with probability in this document) is shown on the vertical axis, and consequence is shown on the horizontal axis (likelihood and consequence categories defined in Tables 1 and 2). Consequences labels on each bar represent the reduction in AIS spread timeline attributed to recreational boating, relative to a natural dispersal baseline. In this scenario, the most likely outcome is a High Consequence (5 y reduction) of boater-mediated AIS spread, which will occur with Moderate Likelihood, while Very High (> 5 y reduction), Moderate (3–5 y reduction), and Low Consequences (1–2 y reduction) will occur with Low Likelihood, and a Very Low Consequence (< 1 y reduction) will occur with Very Low Likelihood. The highest consequence category indicates that upstream boater-mediated spread has occurred.

SCOPE OF RISK ASSESSMENT AND OVERVIEW OF MODEL-BASED APPROACH

This ecological risk assessment involves quantifying the likelihood of spreading AIS within the Canadian and U.S. waters of the Laurentian GLB as a function of recreational boating within the GLB. For the purpose of this assessment, the spatial scale of the GLB includes all waters downstream of the first physical barrier in tributaries (outlined in Cudmore et al. 2017), with the port of Valleyfield, QC as the eastern boundary of the study system. Recreational boats were defined as vessels < 12.2 meters in length used strictly for recreational and non-commercial purposes (definition similar to Rothlisberger et al. 2010); therefore, the assessment covers power-driven boats, such as recreational fishing boats, bowriders, houseboats, and many other classes of power-driven boats, sail-driven boats, such as small and large sailboats, and manually-driven boats, such as kayaks and canoes, but excludes small commercially operated vessels such as barges, tour boats, and commercial fishing boats. The GLB was identified as the region of interest for several reasons, including:

1) ongoing primary introductions of non-indigenous species (Ricciardi 2006; Casas-Monroy et al. 2014, 2015), many of which are known or suspected to be transported by recreational boats (e.g., Johnson et al. 2001; Jacobs and MacIsaac 2007; Rothlisberger et al. 2010);

2) the large volume of recreational boating in the region (e.g., 4.2 M boaters believed to live within border states in the U.S., and 2 M boaters within Ontario and Quebec; Thorp and Stone 2000);

3) the need to compare recreational boater-mediated AIS spread with spread expected through other mechanisms, such as commercial vessels (e.g., Drake et al. 2015b); and,

4) to address scientific uncertainties about the potential for facilitated upstream movements of AIS throughout connecting channels in the GLB.

To provide clarity about terminology used throughout this document, the term 'spread' will be used to encompass the entire process of secondary spread, which involves:

i) the uptake or fouling of organisms that were introduced to a waterbody through a primary or secondary mechanism and occupy a single invaded locality within the GLB (e.g., the nearshore waters surrounding a boat ramp or other recreational site such as a harbour or marina);

ii) the movement (i.e., introduction) of these organisms via recreational boating to beyond the initial invaded locality; and,

iii) the survival and establishment (i.e., development of reproducing populations) beyond the initial invaded locality.

Quantifying these stages temporally and spatially allows a rate of spread involving uptake, movement, release, and establishment to be defined (e.g., recreational harbours invaded per year; time for boater-mediated spread to occur between harbours and lakes).

To understand the potential for AIS spread, a model-based approach was chosen because of the difficulty of deriving empirical rates of boater-mediated AIS spread in systems where multiple pathways of introduction and spread exist. A model-based approach also allowed the lack of data in some steps to be assessed via sensitivity analysis. The model-based approach involved projecting the spread of AIS for three discrete functional groups of organisms known or likely to be transported by recreational boats. Functional groups were not necessarily mutually exclusive and include:

i) plankton or species with planktonic life stages (primarily zooplankton and phytoplankton, e.g., *Bosmina* sp.; *Bythotrephes* sp.);

ii) species with morphological characteristics that facilitate direct attachment onto the hard surfaces of boats or related equipment (primarily molluscs, e.g., adult Zebra Mussel and Quagga Mussel; adult New Zealand Mud Snail ((*Potamopyrgus antipodarum*), but potentially also scud or isopoda like *Apocorophium lacustre*); and,

iii) species lacking direct attachment potential that can be transported inadvertently due to entanglement as a result of their physical characteristics (primarily macrophytes, such as Eurasian Watermilfoil)

To understand the spatial and temporal dynamics of secondary spread attributed to recreational boating in the GLB, the model-based approach involved four main stages:

i) simulating the introduction of species with predetermined functional characteristics and quantifying the interaction between the introduced population and recreational boating activity, such as the probability that a boat becomes contaminated, the density of transported species when contamination occurs, and the pattern of boater-mediated movement (the 'propagule pressure' stage; Figure 2, step 1);

ii) quantifying the relationship between the density of transported species and their potential to establish reproducing populations (Figure 2, step 2);

iii) recording the spread process (uptake, movement, release, establishment across the entire boater population) across a 10 year window (i.e., overall probability of spread stemming from a given origin; Figure 2, step 3); and,

iv) comparing boater-mediated spread timelines with spread expected under natural dispersal (Figure 2, step 4).

KEY ASSUMPTIONS OF MODEL-BASED APPROACH

The model involves several assumptions, which are discussed in detail throughout the document. However, four overarching assumptions and points of clarification are relevant for understanding the implications of this risk assessment. First, because maximum estimates of propagule pressure were used, the model represents a 'worst-case' scenario (i.e. quickest boater-mediated spread timelines derived). For example, it was assumed that boats within a given class (e.g., power-driven boats) and set of operational characteristics (e.g., in-water storage) were equally likely to become infested at the maximum rate and that all propagules survived transport, regardless of variation in individual boater behaviour, such as boat cleaning. Second, it was assumed that environmental factors like climate or site-specific habitat features did not limit the potential for AIS to establish following their initial introduction and establishment; therefore, AIS established within a single locality in the GLB could establish at any site when transported with sufficient propagule pressure to overcome demographic constraints. Third, it was assumed that the parameters chosen for each functional group were representative of the behaviour of each functional group in the GLB. Fourth, as species-specific natural dispersal estimates were unavailable, it was assumed that all functional groups had similar rates of natural dispersal, which was justified due to the relatively sessile nature of each functional group. Assumptions were tested through sensitivity analysis to understand their influence on model certainty and to determine which factors required additional study outside of this risk assessment.

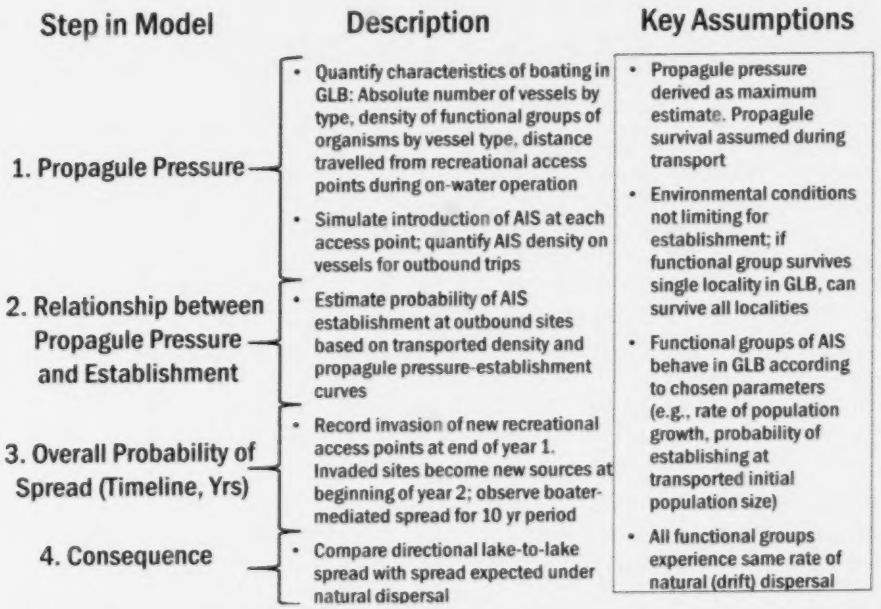

Step in Model
Description
Key Assumptions
1. Propagule Pressure
2. Relationship between Propagule Pressure and Establishment
3. Overall Probability of Spread (Timeline, Yrs)
4. Consequence
• Quantify characteristics of boating in GLB: Absolute number of vessels by type, density of functional groups of organisms by vessel type, distance travelled from recreational access points during on-water operation
• Simulate introduction of AIS at each access point; quantify AIS density on vessels for outbound trips
• Estimate probability of AIS establishment at outbound sites based on transported density and propagule pressure-establishment curves
• Record invasion of new recreational access points at end of year 1. Invaded sites become new sources at beginning of year 2; observe boater-mediated spread for 10 yr period
• Compare directional lake-to-lake spread with spread expected under natural dispersal
• Propagule pressure derived as maximum estimate. Propagule survival assumed during transport
• Environmental conditions not limiting for establishment; if functional group survives single locality in GLB, can survive all localities
• Functional groups of AIS behave in GLB according to chosen parameters (e.g., rate of population growth, probability of establishing at transported initial population size)
• All functional groups experience same rate of natural (drift) dispersal

Figure 2. Overview of the model-based assessment and key assumptions.

ESTIMATING PROPAGULE PRESSURE FROM RECREATIONAL BOATING IN THE GLB

Quantifying the potential for secondary spread is a function of the number of recreational boating trips operating within the GLB, the movement potential of individual boating trips, physical characteristics of boats including variation in operator characteristics (e.g., extent of in-water storage, excursion length and duration) leading to fouling, plus the physical characteristics of organisms that facilitate fouling. Each stage was used to estimate the overall rate and density of organisms transported, the spatial trajectory of an individual boat movement, and the timing of these events. Stages involving the boater-mediated movement of AIS are generically referred to in this document as propagule pressure, which encompasses the rate and magnitude of propagule releases (Lockwood et al. 2005, Drake et al. 2015a).

CHARACTERISTICS OF RECREATIONAL BOATING IN THE GLB

To understand the characteristics of recreational boating in the GLB as they relate to the secondary spread of AIS, a social survey was undertaken in partnership with the Ontario Ministry of Natural Resources and Forestry. The survey involved mail-out delivery of 6,000 paper copies during March 2010 to households in proximity to the GLB, as well as an online component hosted at a SurveyMonkey website (responses collected between March and September 2010) and advertised at the Sportsman's Show in Toronto during spring 2010 (see Appendix 1 for survey content). The goal of the survey was to understand the characteristics of boating activity during the 2009 calendar year, including the characteristics of boats used in the GLB (e.g., manually driven vs power-driven; length of boat), the number of times an operator used a boat within the Great Lakes, spatial aspects of boating trips (e.g., port-to-port movements vs distance of local cruising), and the frequency with which activities to discourage fouling were undertaken, such as cleaning or inspection of equipment. The mail-out survey was designed to sample licenced anglers, many of whom boat either as part of, or separately from, angling activities, while another population was sampled from advertisements distributed at the Sportsman's Show, representing a broader spectrum of boaters, anglers, and other outdoor enthusiasts.

A total of 1,496 survey responses were collected, but only 767 individuals (51.3%) indicated owning and using a recreational boat in 2009. Of these active boaters, 234 (30.5%) indicated that they undertook boating activities within the GLB during 2009 (Table 4). Boater characteristics relevant to secondary spread in the GLB were summarized from the survey, with most parameters calculated as proportions. For example, the proportion of respondents who stored their boat in the water was lower for GL-specific respondents (0.18) than the overall surveyed average (0.22; Table 4). Nearly 40% of respondents that indicated using their boat in the GLB during 2009 also used the same boat in inland waters, and a subset of GLB boaters also indicated using their GLB boat beyond Ontario and the Great Lakes during the surveyed year (3.4%). The proportion of GLB boaters that always or sometimes took steps to clean their boats ranged from a high of 37.6% for individuals stating that they dried their boat and related components for at least five days, to a low of 4.7% for individuals who reported flushing motor intakes. However, the overall proportion of GLB boaters that always or sometimes took at least one step to clean their boat and related equipment was 68%, signifying moderate participation in at least one cleaning step (Table 4).

Table 4. Responses from the Ontario Recreational Boater Survey, which was distributed to users between March and September, 2010. The survey asked boaters to describe their trip, boat, and behavioural characteristics for the 2009 boating season.

Surveyed Question	Overall	Great Lakes Specific
Proportion of respondents that indicated owning and using a boat in the survey year (includes both GLB and inland activity; hereafter, 'active' users)	767/1,496 respondents = 0.512	-
Proportion of users indicating at least some level of boating activity in GLB, given that they were active users	-	234/767 = 0.305
Proportion of active users that stored boat in water at marina or in water at principal residence	173/767 = 0.225	43/234 = 0.183
Proportion of GL boaters that used boat in inland waters	-	94/234 = 0.401
Proportion of boaters that used boat in waters beyond Ontario and the Great Lakes	25/767 = 0.032	8/234 = 0.034
Proportion of boaters that reported always or sometimes:		
Removing plants and animals by visual inspection	150/767 = 0.195	48/234 = 0.205
Purposefully draining boat areas that accumulate water (bilge, livewell, etc.)	77/767 = 0.100	23/234 = 0.098
Completely drying boat and related components for 5 days or more	229/767 = 0.298	88/234 = 0.376
Rinsing boat and related equipment with high pressure water	230/767 = 0.299	87/234 = 0.371
Rinsing boat and related equipment with hot water	68/767 = 0.088	24/234 = 0.102
Cleaning anchor, anchor line, and related components	107/767 = 0.139	25/234 = 0.106
Cleaning downrigger, fishing line, and related components	61/767 = 0.079	23/234 = 0.098
Flushing motor intake (i.e., cooling system)	39/767 = 0.050	11/234 = 0.047
Conducting at least one of the cleaning steps presented above	491/767 = 0.640	161/234 = 0.688

Additional trip characteristics of active GLB boaters were recorded, such as the class of boat used during the total number of trips (power-driven: 81.7% of trips, manually driven (e.g., canoe-kayak), 13.9% of trips, and sailboat: 4.3% of trips), the size-frequency distribution of boats used in 2009 (less than 12 feet: 14.3% of trips, 12–15 feet: 31.9% of trips, 16–20 feet: 37.3% of trips, 21–27 feet: 12.5% of trips, 28–40 feet: 3.7% of trips and > 40 feet: 0.36% of trips), and the proportion of surveyed respondents that indicated fishing during an individual trip (a maximum 82.4% of trips). Active boaters in the GLB reported taking an average of 8.8 trips per year, which was similar to the overall surveyed average of 8.7 trips/y. Based on Akaike's Information Criterion (AIC), the most parsimonious statistical distribution to describe the frequency distribution of GLB boating trips taken by an individual user was a negative binomial distribution, with parameters of $k = 1.07$, $\mu = 8.84$ derived through maximum likelihood.

Significance tests were conducted to determine whether certain boating activities occurred more or less frequently in relation to mean on-water trip distances (methods to estimate mean distance described below). This step was also necessary to determine if mean trip lengths varied with certain boat classes (e.g., powerboat vs manually driven boat vs sailboat; Table 5), for certain geographic regions (Table 6), or in relation to certain risky behaviours, such as lack of cleaning (Figure 3; $p > 0.05$). Results of significance tests indicated that sail-powered boats and motor-powered boats generally traveled consistent distances, but sail-powered boats and manually-powered boats (e.g., canoes, kayaks), and motor-powered boats and manually powered boats, had different mean travel distances ($p < 0.05$; Table 5). Results of significance testing also indicated that boaters tend to travel similar mean on-water distances with only minor geographic variation (Table 6; pairwise comparisons revealed only three significant broad geographic pairings). Decisions to undertake boat cleaning generally occurred irrespective of distance travelled ($p > 0.05$; Figure 3). The results of significance testing informed subsequent stages of the spread model in which the rate and magnitude of propagule pressure was simulated in relation to travel distance.

Quantifying the potential for boater-mediated movement of AIS also involved estimating the potential for offshore vs nearshore trips. These loosely defined trip choices were not compiled as part of the survey and it was initially assumed that each type of trip was equally likely in the GLB (e.g., probability of traveling along the shoreline = 0.5, probability of not traveling along the shoreline = 0.5), though the effect of these assumptions were validated through sensitivity analysis. Nearshore trips, defined as those transiting within 1 km of the shoreline and thus in proximity to potential recreational access sites, were of interest as most likely contributing to the stepping-stone pattern of secondary spread expected in the GLB (e.g., offshore trips and related propagules assumed to 'drop out' of the model). The probability of undertaking an international trip or of transiting through lock structures in the GLB was also estimated. International trips were defined as trips originating at a given recreational site that involved visiting a second recreational access site in a different country. Transiting through lock structures considered the potential for travel through the Welland Canal system or the Sault Ste. Marie Canal system in the St. Lawrence Seaway. As the survey did not encompass international or lock-transitioning behaviour, it was assumed that the maximum rate of undertaking either activity could have occurred, in theory, during an additional collected survey response, which would define the maximum probability with which these activities occurred. Therefore, each step (international trips, through-lock trips) were assumed to occur with a probability of 1/(1+234), signifying that the next surveyed individual could have, in theory, undertaken each activity. The effect of each assumption was quantified through sensitivity analysis.

Table 5. Tukey HSD significance values, with mean reported distance as a function of boat type (overall $p < 0.001$).

	Estimate	Adjusted p-value
Powerboat - Manual	13.94	0.0001
Sailboat - Manual	8.09	0.019
Sailboat - Powerboat	-5.84	0.076

*Table 6. Tukey HSD significance values, with mean reported distance as a function of postal district of respondent (overall $p < 0.001$). Postal districts are L = Greater Toronto Area, N = Southwestern Ontario, K = Southeastern Ontario, M = Metropolitan Toronto, and P = Northern Ontario. A * indicates a significant comparison at $\alpha = 0.05$.*

Postal District Comparisons	Difference	Adjusted p-value
L-K	0.208	0.009*
M-K	0.340	0.57
N-K	-0.069	0.91
P-K	0.0005	1.0
M-L	0.131	0.977
N-L	-0.278	0.001*
P-L	-0.208	0.0022*
N-M	-0.410	0.361
P-M	-0.340	0.565
P-N	0.070	0.736

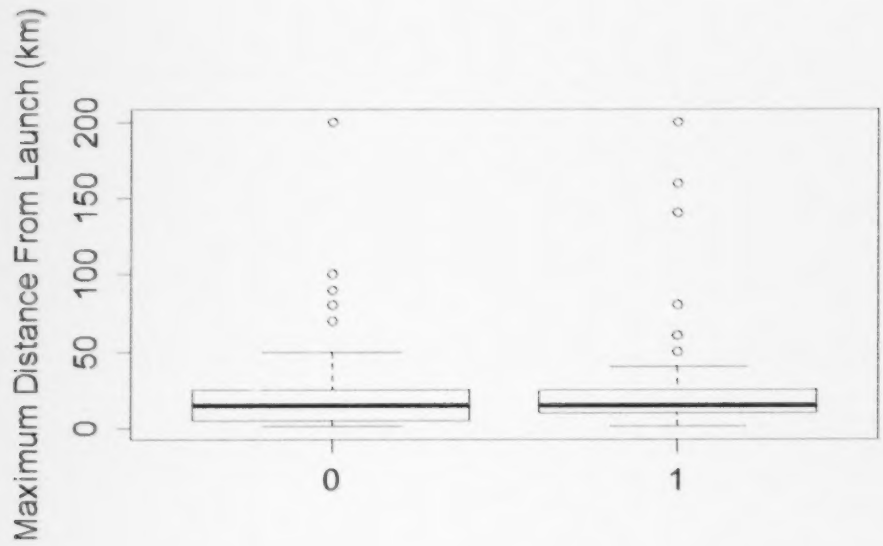


Figure 3. Maximum distances travelled from launch in the Great Lakes reported by boaters who do not undertake any cleaning steps (0) vs boaters who undertake at least one cleaning step (1).

ESTIMATING THE FREQUENCY AND SPATIAL DISTRIBUTION OF RECREATIONAL BOATING IN THE GLB

Estimating the yearly frequency and spatial distribution of recreational boating trips in the GLB involved quantifying the total number of boating trips in the Canadian and American waters of the GLB in the surveyed year (where a 'trip' is defined as a boating event occurring within a single day), as well as forecasting the spatial trajectory of individual trips given the movement characteristics identified in the Ontario boater social survey. Trip frequency and movement information was combined with additional trip characteristics obtained from the Ontario survey (e.g., the type of boat, frequency of in-water storage) to determine the potential for fouling with functional groups of organisms (see functional group section).

To quantify the yearly number of recreational boating trips in the GLB, data from the U.S. Army Corps of Engineers (2008) were used to quantify the relationship between:

i) the total number of recreational boats owned and/or registered within the eight Great Lakes states; and

ii) the proportion of these boats that were used in the Great Lakes (as opposed to being used exclusively in inland waters within Great Lakes states) in a given year (Table 7).

Data existed for the total number of boats owned in Ontario and Quebec (Thorp and Stone 2000), but not for the subset of Ontario and Quebec boats that were used in the Great Lakes proper. However, the proportion derived for the U.S. (total boats vs subset of boats used in GLB) was assumed to hold for Canadian populations, allowing the total number of Canadian boats used in the Great Lakes in a given year to be quantified. Data describing the total number of Canadian and U.S. boats used in the Great Lakes in a given year were multiplied by the survey-derived mean number of trips per boater per year, leading to an overall estimated number of recreational boating trips within the Great Lakes in a given year (11.8 M in total; 3.8 M in Canada; 8.0 M in the United States; Table 7).

To quantify the physical origin of boating trips, which typically involve launch ramps and/or recreational harbours, data on the spatial distribution of recreational access points encompassing marinas, boat ramps, and recreational harbours were compiled from several GIS sources (most data were collected by Canadian federal and provincial initiatives to support GLB research initiatives; Figure 4). These data provided an approximation of operating recreational access points in the Great Lakes (1,717 in total; 487 in Canadian waters, 1,230 in U.S. waters; Figure 4).

Because data collected through the social survey did not attempt to characterize the motivations for launching or mooring at specific locations within the GLB, the utilization of individual access points was unknown. If each access point was equally likely to support a given trip, the total number of GLB trips (3.8 M Canada, 8.0 M U.S.) partitioned across available access points would lead to 7,804 trips originating at each access site in Canada and 6,504 trips originating at each access site in the United States. However, because the number of trips departing from access points inevitably displays spatial structuring in relation to site choice attributes, such as proximity from boater residences and other social and economic factors, a negative binomial distribution (k = 1) was incorporated to reflect uncertainty in the intensity of recreational site use across the GLB landscape. The mean value of the negative binomial distribution, representing the average number of trips originating from any Canadian or U.S. access point, was equal to the number of trips that should occur if sites were equally attractive (7,804 Canada, 6,504 U.S.). This statistical approach allowed for strong spatial variation in the intensity of access point usage during model simulations, where certain sites in certain years were characterized by a disproportionately high amount of boater activity.

Table 7. Estimated yearly total number of recreational boating trips within the Great Lakes basin. Total number of trips per year was estimated (D) as = (A x B) x 8.8 trips/y.

	A: Boats owned in provinces (ON, QC) or states (MN, MI, IL, IN, PA, WI, NY, OH) bordering Great Lakes	B: Proportion of boats using GL in a given year	C: Total number of recreational boats using GL	D: Estimated total number of trips (~boater days) within GL (based on mean of 8.8 trips/y/boater)	Proportion of total GLB trips originating from Canada vs U.S. origins
Canada	2.0 million	0.216	432,000	3.80 million	0.32
U.S.	4.2 million	0.216	911,000	8.01 million	0.68
Total	6.2 million	-	1.3 million	11.81 million	1.0

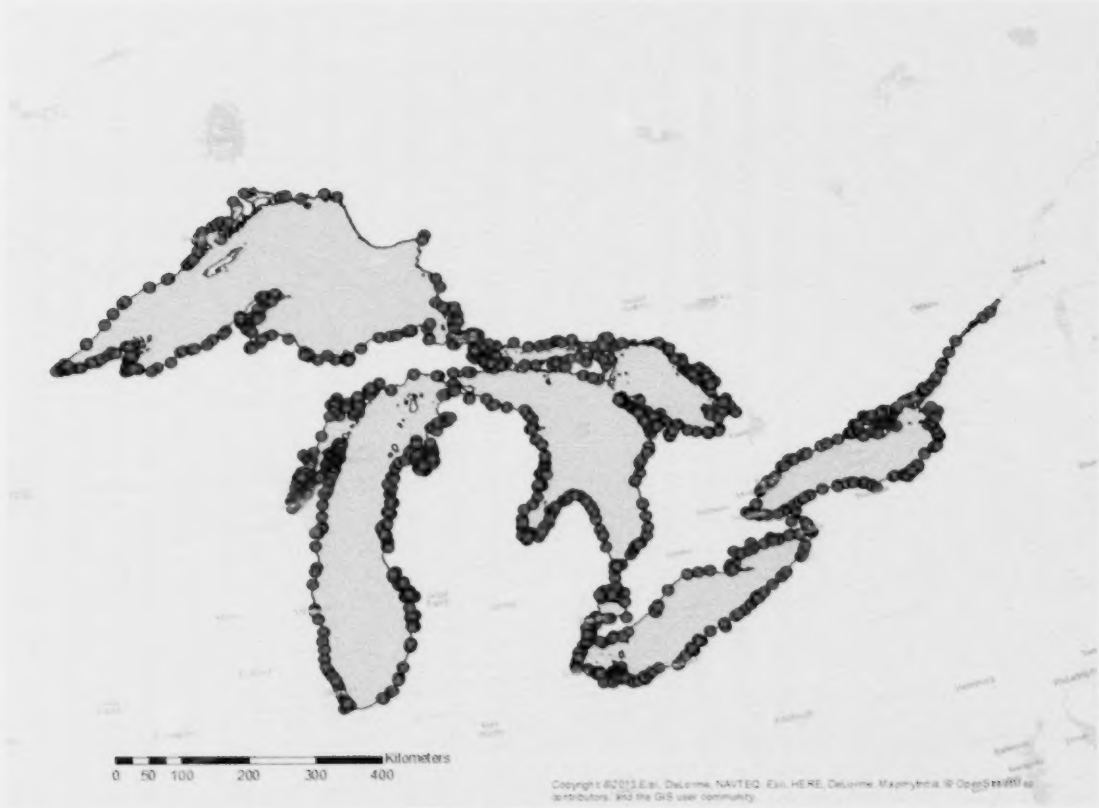


Figure 4. Spatial distribution of the 1,717 recreational access points distributed throughout the Great Lakes basin. A total of 487 recreational access points were located in Canada and 1,230 were located in the U.S.

To relate each of the 11.8 M yearly trips to on-water movements, a statistical dispersal kernel was developed and parameterized through survey data. The dispersal kernel was used to describe the probability that an individual trip would travel a given on-water distance from the recreational access site, providing a measure of the movement of AIS when a trip was contaminated. For up to ten possible trip scenarios, survey respondents reported the waterbody where their GLB trip occurred (e.g., Georgian Bay), the destination of their trip (e.g., Parry Island), the approximate total round-trip length of their trip (e.g., 80 km), and the approximate number of times this specific route was taken in 2009. An option allowed boaters to choose "NA – only boated locally", rather than providing a specific destination location, which was chosen the majority of the time. When destinations were reported, they were often generic landmarks (e.g., Seagull Rock) that could not be positively identified; therefore, in all cases the round-trip length of each trip was used to construct the dispersal kernel.

To estimate parameters of the dispersal kernel, data describing absolute frequency vs total travel distance were compiled. Each trip distance (i.e., total round-trip distance) was divided by a value of two, providing the greatest possible outbound travel distance from a launch site. This approach provided the travel distances expected if all trips followed a Euclidean (i.e., straight-line) path outbound from the recreational access site. A random-walk type of trip would lead to a smaller maximum extent of travel, so this approach provided the greatest possible distance

travelled given uncertainties in fine-scale movement characteristics. The resulting travel distances were plotted as a histogram (Figure 5), reflecting the empirical distribution of assumed maximum Euclidean distances travelled from the recreational access site. The probability distribution underlying this dispersal kernel was evaluated using Akaike's Information Criterion (AIC), and the lowest AIC value was associated with a log-normal distribution, resulting in a dispersal kernel with parameters $\mu_{log} = 1.93$ and $\sigma_{log} = 0.94$ (Figure 6). Based on this statistical dispersal kernel, the most likely travel distance from launch was approximately 3 km, the probability of travelling > 10 km from launch was p = 0.35, while the probability of travelling > 100 km was p = 0.0022. For illustrative purposes, given a total of 11.8 M trips occurring in the GLB each year, at least 26,303 yearly trips, on average, would travel distances of approximately 100 km from launch, and 31 trips would travel distances of about 500 km from launch. An example of the probability of moving a given distance from a launch site in Thunder Bay, ON is shown in Figure 6. Note that the use of a single dispersal kernel overestimated the distances travelled by manually-driven boats, but these boats had disproportionately low propagule pressure compared to other boat classes. Given this trade-off, the error associated with a single dispersal kernel was assumed to be low.

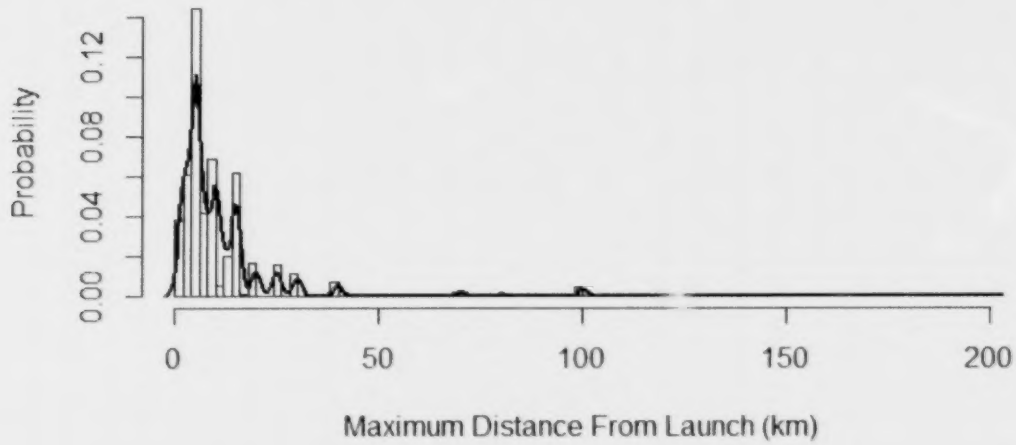


Figure 5. Observed distance-frequency histogram of recreational boating trips in the Great Lakes. Data were based on n = 2501 trips occurring in the Great Lakes proper as reported by 234 survey respondents. Distances represent the half-length of round trips that were self-reported. Reproduced from Drake et al. 2015b.

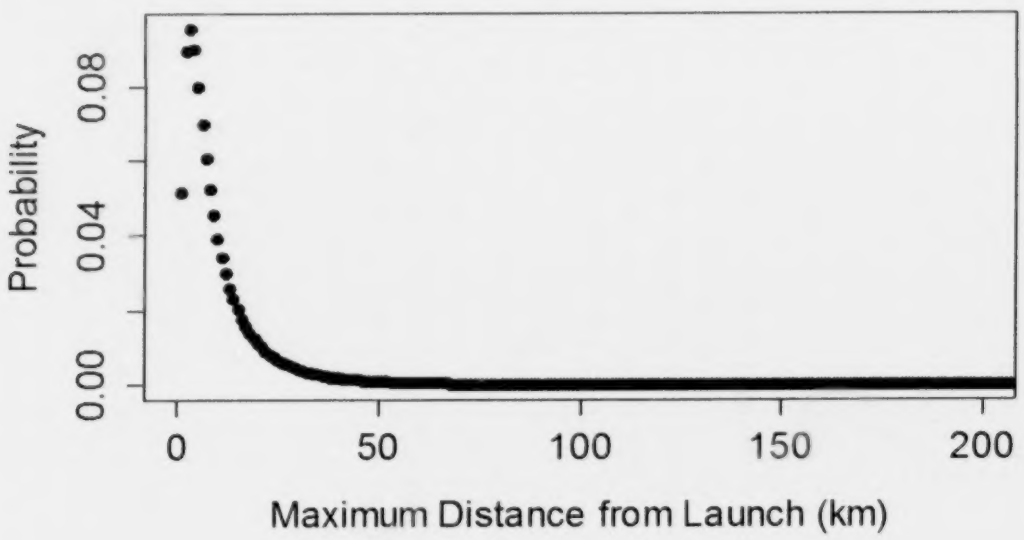


Figure 6. Log-normal statistical dispersal kernel based on empirical survey data. The most parsimonious model to describe the distance-frequency distribution was a log-normal distribution with parameters μ_{log} = 1.93 and σ_{log} = 0.94.

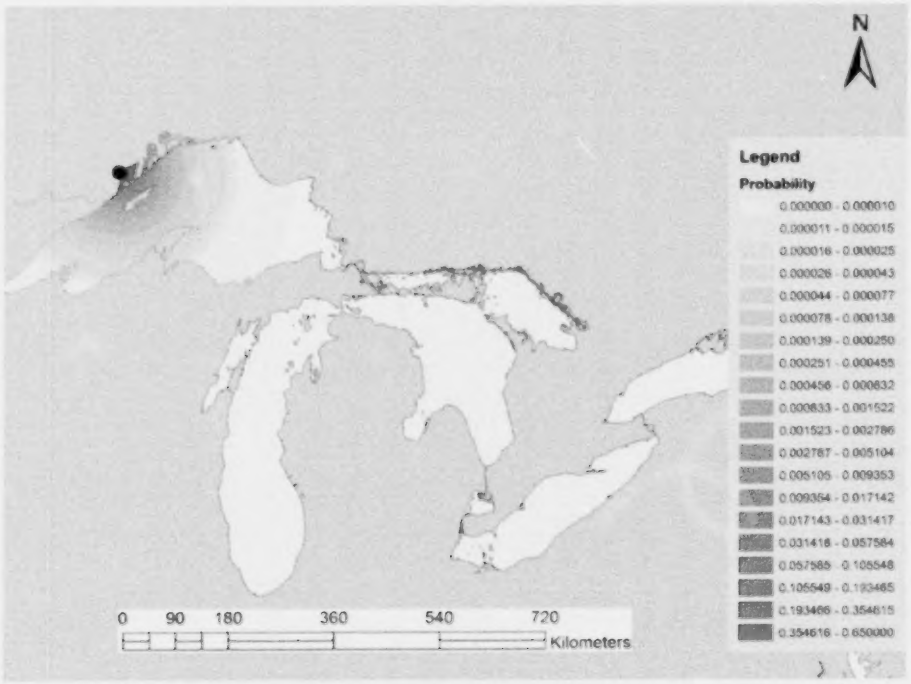


Figure 7. Statistical dispersal kernel (log-normal distribution with μ_{log} = 1.93 and σ_{log} = 0.94) used to quantify recreational boater movement. Shown are trips originating from Thunder Bay, Ontario as source location (marked with black circle). Note relative probability legend (all pale yellow values represent negligible probability of movement from origin). Reproduced from Drake et al. 2015b.

FUNCTIONAL GROUPS OF AIS LIKELY TO BE TRANSPORTED BY RECREATIONAL BOATS IN FRESHWATER ECOSYSTEMS

Following development of the statistical dispersal kernel, the functional groups of AIS likely to be transported by recreational boats in the GLB were quantified. Based on a literature review of aquatic species commonly fouled on recreational boats (Drake 2017), three functional groups of freshwater organisms were identified as potentially transported by recreational boats. These functional groups were not mutually exclusive but represent different classes of organisms that can occur on or within boat components (e.g., hull attachment, entrainment within engine cooling water or livewells, infestation of accessory surfaces) due to physical and ecological characteristics. Functional groups were:

1) plankton (phytoplankton and zooplankton, such as the juvenile or adult stages of species such as Spiny Waterflea and Fishhook Waterflea) or organisms with planktonic life stages (e.g., the veliger stage of Zebra Mussel and Quagga Mussel);
2) non-planktonic organisms or life stages having specialized structures that allow direct, semi-permanent attachment onto boats or related equipment (e.g., molluscs: adult Zebra Mussel or Quagga Mussel; adult New Zealand Mud Snail); and,
3) aquatic macrophytes that may be inadvertently transported on or in boats or related equipment (e.g., Eurasian Watermilfoil tangled with anchor lines or transported inadvertently within livewells).

This classification does not capture the benthic life stages of certain species and their transport mechanisms (e.g., benthic larvae transported via anchor sediments), which may also be a potentially important source of human-mediated spread within the basin.

A literature review of functional groups was used to quantify the physical locations on boats where organisms have been reported, their greatest mean density (propagules/m^3 or m^2) on or in physical boat structures, and, in some cases, the baseline density of organisms in surrounding waters (Table 8).

Table 8. Characteristics of functional groups of AIS transported by recreational boats across North America. Reported variables include transported density and contamination location on each boat, as well as geographic scope.

Organism	Propagule Density (mean organisms/m^3 unless noted)	Location on Boat	Geographic Scope	Reference
Zebra Mussel (veligers)	16/L or 16,000/m^3 5.9/L or 5,900/m^3 19/L 19,000/m^3 7.9/L or 7,900/m^3	Engine cooling system Bilge Livewell Bait bucket	Arriving to Lake St. Clair boat launches, U.S.	Johnson et al. (2001)
Zebra Mussel (veligers)	19/0.47L or 40,280/m^3	Engine cooling system	Lake Mead and Lake Powell, U.S.	Dalton and Cottrell (2013)

Organism	Propagule Density (mean organisms/m^3 unless noted)	Location on Boat	Geographic Scope	Reference
Zebra Mussel (adults)	44,000/m^2 15,000/m^2 5,000/m^2 4,500/m^2 3,000/m^2 1,000/m^2 1,000/m^2 500/m^2	Outside of hull: barge Tug Others vessel classes Private cruiser Canal boat Lake boat Yacht Dinghy	Shannon, Grand Canal, Lough Erne in Ireland	Minchin et al. (2003)
Zebra Mussel (veligers)	25,000/m^3	NA: Baseline density in surface waters around boat launches	Lake St. Clair, U.S.	Johnson et al. (2001)
Zebra Mussel (veligers)	31,000/m^3	NA: Baseline peak density observed in Lake Michigan	Lake Michigan, U.S.	Dalton and Cottrell (2013)
New Zealand Mud Snail (adults)	5,600/m^2	NA: Baseline density observed in Lake Erie	Lake Erie, U.S.	Levri et al. (2007)
Zebra Mussel (adults)	~20,000/m^2	NA: Baseline density observed in Upper St. Lawrence River	St. Lawrence River, Canada	Ricciardi et al. 1998
Spiny Waterflea / Fishhook Waterflea (adults)	59, 9, 50, 46 per line (10 m) 381, 30, 149, 259 (20 m)	Downrigger cables and fishing line, 10 and 20 m depth	Western end of Lake Ontario, Canada, 1–2 km offshore	Jacobs and MacIsaac 2007
Spiny Waterflea / Fishhook Waterflea (adults)	57/m^3 (10 m depth), 81/m^3 (20 m), 262/m^3 (20m)	10 and 20 m depth of baseline density in Lake Ontario adjacent to fishing line tests	Western end of Lake Ontario, Canada, 1–2 km offshore from Burlington	Jacobs and MacIsaac (2007)
Several native zooplankton spp., plus Zebra Mussel veligers	Pelagic Zoo spp. = 2700/m^3 Littoral Zoo spp. = 100/m^3 Benthic Zoo spp. = 100/m^3 Zebra Mussel = 200/m^3	Bilge (n = 19) Anchor bracket (n = 1) Small area behind engine (n = 1) Other localities: 21 out of 63 boats contained standing water that was sampled.	Lake Simcoe, Ontario, Canada	Kelly et al. (2013)

Organism	Propagule Density (mean organisms/m^3 unless noted)	Location on Boat	Geographic Scope	Reference
Macrophyte fragments (native species, including *Myriophylum* sp.)	N/A: 31 of 49 boats had fragments, but 2 of 49 boats had fragments above weight threshold for viability (35 g)	All exterior surfaces sampled	Big St. Germain Lake, northern Wisconsin and Lake Gogebic, upper Peninsula of Michigan, U.S.	Rothlisberger et al. (2010) (see Table 2 for range of species)
Macrophyte fragments (native spp.)	N/A: Based on macrophyte fouling score/index. 7 of 63 boats had score of 1 (lowest level of fouling; proportion = 0.11), and 1 or 63 boats had score of 3 (highest = 0.015).	All exterior surfaces. Most fragments found on anchor line.	Lake Simcoe, Ontario, Canada	Kelly et al. (2013)
Macrophytes (whole plants – Eurasian Watermilfoil)	300 plant stems per m^2 of benthic habitat	NA: Baseline peak density in benthic environment	Canadian lakes	Aiken et al. (1979)

For planktonic organisms, Johnson et al. (2001) found that veliger (i.e., planktonic) densities of Zebra Mussel occurred in highest mean concentrations within livewells and engine cooling water for boats sampled at the end of day-use trips in nearshore areas of Lake St. Clair, U.S.. Similar findings were described by Dalton and Cottrell (2013), who reported the highest densities of planktonic organisms (Zebra Mussel veligers) in engine cooling water for boats sampled near Lake Mead U.S., at densities of > 40,000/m^3. A key conclusion from both studies was that the density of plankton within boat structures was generally consistent with the mean density of plankton in the surrounding surface waters (e.g., 16,000 – 19,000 veligers/m^3 in cooling water and livewells vs 25,000 veligers/m^3 in open waters of Lake St. Clair (Johnson et al. [2001]; 40,280 veligers/m^3 in boat cooling water from Lake Mead vs 31,000 veligers/m^3 for peak density in Lake Michigan [Dalton and Cottrell 2013]). For physical boat structures other than engine cooling water and livewells, Kelly et al. (2013) found relatively low densities of larval Zebra Mussel in bilge water (200 veligers/m^3) for boats transiting within waters infested with Zebra Mussel, but densities of native pelagic plankton within bilge and other standing water areas were quite high (e.g., 2,700 native pelagic zooplankton individuals/m^3).

The propagule concentrations obtained from the literature were used to quantify the relationship between plankton density in the waters surrounding a recreational access site with the expected density of propagules transported by different boat structures. For example, all boats with outboard or inboard engines would be capable of transporting plankton at densities generally consistent with their surrounding environment, as would those with livewells or other pumping devices (e.g., flushing stations). These findings indicate that engine cooling water and livewell-type structures lead to the greatest potential estimate of propagule size (measured as density) for an individual boat. Density of propagules in bilge and other standing water were lower, indicating that manually powered boats, primarily canoes and kayaks in the GLB, likely contained concentrations of plankton at roughly ten-times less the concentrations in surrounding

surface waters (Table 9). These relationships formed the basis for estimating propagule sizes for the plankton functional class during individual trips within the GLB.

Table 9. Summary of plankton fouling densities for boat classes operating within the GLB.

Boat Class	Occurrence of Planktonic Organisms in Engine Cooling Water or Similar Structures (e.g., livewells).	Maximum Density of Planktonic Organisms
Power-driven boat	Yes	Approximately consistent with surface waters
Sail-driven boat	Yes	Approximately consistent with surface waters
Manually-driven boat	No	~10 times less than surface waters

For organisms that can exhibit direct, semi-permanent attachment onto boats (e.g., adult Zebra Mussel and Quagga Mussel, adult New Zealand Mud Snail), few North American studies have documented direct fouling of recreational boats. For example, Johnson et al. (2001) reported that most adult Zebra Mussel found on day-launch boats were entangled within aquatic macrophytes that were fouled with Zebra Mussel (i.e., the authors found few adult mussels attached directly to boat surfaces). However, Minchin et al. (2003) documented densities of Zebra Mussel of between 500 per m^2 and 44,000 per m^2 on the outside of recreational and commercial hulls in freshwater lakes in Ireland. In that study, ships stored in-water exhibited the highest degree of fouling (e.g., 44,000 molluscs per m^2 on hull surfaces); whereas, ships stored infrequently in-water, or those dried regularly, contained the lowest densities (500 molluscs per m^2 of hull surface). In general, these findings support the hypothesis that for organisms with direct attachment potential, greatest fouling density will occur when boats have been left in the water for lengthy periods of time. A relatively modest proportion of trips in the GLB involve in-water storage (18.3%) for active GLB boaters. Although the density of adult Zebra Mussel in North American lakes is highly variable (Ricciardi et al. 1998 documented benthic densities across North America ranging from 3,000 to over 100,000 organisms/m^2), findings from Minchin et al. (2003) indicate that in-water storage can support densities consistent with the surrounding environment, while day-launch trips tend to support densities that occur at roughly 11% of surrounding densities.

Given these findings, two distinct scenarios exist for the direct fouling of recreational boats by the mollusc functional group:

1) fouling that occurs frequently and with high organism density resulting from in-water boat storage; and,
2) fouling that occurs infrequently and with low organism density for day-launch trips (i.e., trips lacking in-water storage).

For fouling based on in-water storage, the probability of a trip involving in-water storage in the GLB (0.183) was used to estimate the proportion of boats that would experience the greatest degree of fouling, which was assumed to occur at maximum observed organism density in the GLB. This approach provides a maximum estimate of fouling, recognizing that some boats and trips may involve steps such as cleaning to remove mussels (though cleaning and other antifouling techniques are rarely uniformly effective). Therefore, a maximum estimate of risk was chosen where in-water storage leads to the highest degree of fouling, irrespective of cleaning

practices. For remaining boats that are day launched (i.e., 1 minus the number of boats stored in-water,
1 - 0.183 = 0.817), the rate of direct fouling was calculated based on observations of fouling for day launched boats in nearshore Lake St. Clair (Johnson et al. 2001). The probability of a day-launch trip becoming fouled was calculated by identifying the total sample size of GLB boats that were sampled for fouling by Johnson et al. (2001) (822 boats; all boats found not to be fouled), adding 1 to reflect that fouling could have been discovered during the next sample (the 823rd boat, in theory), and dividing 1 by this value to obtain the overall maximum probability of direct fouling (1 / (1 + the number found not to be fouled)). The resulting maximum probability of a day-launched boat being fouled (0.0012), multiplied by the probability of not being stored in-water (1-0.183), resulted in an overall probability of a day-launch trip becoming fouled (p = 0.0009186; Table 10). Should a day-launch boat become fouled, the fouled organism density was obtained by multiplying densities found in GLB benthic environments by 0.11, which reflected the proportional reduction in density seen in Minchin et al. 2003 for smaller, day-launch type boats.

Table 10. Estimated fouling rate and density of the mollusc functional group for boats operating within the GLB.

Boat Class	Prevalence of Trip Type and Rate of Colonization	Maximum Density of Organisms When Fouling Occurs
Stored in-water	0.183 (proportion of in-water storage; all in-water storage assumed to exhibit fouling)	Approximately consistent with benthic density
Day-launch (i.e., dry-land storage)	0.817 (proportion of day-launch trip) x 0.0012 (rate of colonization for day-launch trip) = 0.00091	Benthic density x 0.11 (reduction for day-launch boats compared with in-water storage; Minchin et al. 2003)

To quantify the fouling potential of the macrophyte functional class, empirical data were used to quantify the overall probability that a recreational boat would become fouled with viable plant fragments. Rothlisberger et al. (2010) found that 31 of 49 boats had native macrophyte fragments contained within boat surfaces (e.g., bilge water) when leaving small inland lakes in Wisconsin, but only 2 of 49 had fragments that were large enough to be considered viable if released to the water. Kelly et al. (2013) sampled native macrophyte fragments from recreational boats travelling within Lake Simcoe (a large inland lake with characteristics similar to the GLB). In their study, entanglement of most macrophytes occurred on anchor lines and other structures. As with Rothlisberger et al. (2010), fouling occurred at a generally low rate (1 of 63 boats had fouling that could be considered sufficient to give rise to new plant populations if released). However, based on these studies, there were insufficient data to quantify differences in macrophyte fouling for in-water vs day-launch boater trips; therefore, the maximum rate of fouling from Rothlisberger et al. 2010, 2 of 49 boats (p = 0.041) was applied across all trips and used to estimate the maximum probability that a boat would become fouled with viable fragments. Given observed densities of Eurasian Watermilfoil in the environment of 300 plants/m^2 (Aiken et al. 1979), and the observation of only single viable fragments when boats were fouled, a reduction of 0.0033 for the number of 'viable' plant fragments contained on a boat's surface was assumed (1 fragment observed given 300 stems per m^2 in benthic environment). This reduction was used to quantify the density of macrophytes fouled on boats as a function of the density that exists in the surrounding environment (Table 11).

Table 11. Estimated fouling rate and density of the macrophyte functional class for boats within the GLB.

Maximum Rate of Fouling	Density of Plant Fragments on Boat Surfaces
0.041 (all trip types treated equally)	Reduction of 0.0033 from density in the environment

For an individual boating trip, it was also necessary to calculate the likelihood that organisms from each functional class would be physically dispersed into the water during a single voyage. For planktonic species, there are many scenarios where organism release can occur (e.g., dumping livewells during the voyage; flushing of bilge water; continual flushing of engine cooling water). For species with direct attachment potential, the potential for physical release may range from highly variable to relatively constant throughout a voyage, dictated by boat speed and other hydrodynamic forces. For macrophytes, physical release can be a function of the use of fouled equipment (e.g., anchors), which may also occur during any part of a voyage. As the rate with which these activities occurred was unknown, a generic estimate of p release = 0.5 was made, where organisms were considered to be released with p = 0.5 during visits to nearshore waters (see calculating overall probability of spread for full model development and relevance of nearshore visitation). The effect of choosing p release = 0.5 was explored through sensitivity analysis.

PROBABILITY OF AIS SURVIVAL AND ESTABLISHMENT FOLLOWING BOATER-MEDIATED SECONDARY SPREAD IN THE GLB

Quantifying the relationship between propagule pressure and the probability of establishment is a current challenge in invasion biology (Wonham et al. 2013); however, several modeling approaches exist to describe the functional form of the 'risk-release' relationship. In the context of a recreational boating trip, this relationship describes how the density of organisms transported by individual boats (i.e., propagule sizes) lead to self-sustaining populations of AIS beyond the original invaded location. Although there is uncertainty about the relevance of Allee effects in these relationships (e.g., Wonham et al. 2013), the theory underlying propagule pressure indicates that a higher density of organisms transported will lead to a higher probability of establishment, as the large population sizes introduced reduce the importance of environmental and demographic stochasticity (Lockwood et al. 2005).

Quantifying the probability of AIS establishment involved relating the density of released propagules with the likelihood of establishing viable populations based on the potential to overcome demographic thresholds Variation in environmental factors among receiving sites was considered to not be limiting for establishment. It was assumed that AIS with the potential to establish at a single recreational access site could establish at any recreational access site if propagule pressure was sufficient to overcome demographic thresholds.

RELATIONSHIP BETWEEN PROPAGULE PRESSURE AND ESTABLISHMENT

Approaches to quantify the risk-release relationship are reviewed in Leung et al. (2004), National Research Council (2011), and Wonham et al. (2013). These relationships require a statistical estimate of propagule size (e.g., Drake et al. 2015a), the probability of an individual propagule establishing (a mathematical and not a 'biological' parameter), and the extent of Allee effects as model inputs. The functional-form of the risk-release relationship in Leung et al. (2004) was incorporated where the probability of establishment ($P(E)$) at a given initial population size (N_t) is $PE(N_t) = 1 - e^{-(\alpha N t)^{\wedge c}}$, where α is the natural logarithm of the per-propagule

probability of establishing, and c describes the existence of an Allee effect (c becoming larger than 1 indicates an increasing Allee effect). The term N_t can be considered as the density of propagules released by an individual recreational boat during a trip.

Parameterizing the risk-release relationship involved using the results of a GLB mesocosm experiment conducted in Hamilton Harbour, Lake Ontario (Bailey et al. 2009) to understand the dynamics of invasive plankton at low population sizes, thereby allowing ground-truthing of establishment parameters in the GLB. The mesocosm experiment was developed to determine the overall probability of establishment of plankton inoculated at different initial population sizes (organisms/m^3). The highest alpha value (α) from the mesocosm experiment for invasive, parthenogenetic zooplankton was selected, where the value of $\alpha = 0.1$ was equal to the probability that a single parthenogenetic propagule established in the experiment. This α value was used to relate the density of AIS propagules transported by recreational boats to the establishment probabilities known in the GLB. This value of α was used to quantify the greatest possible probability of establishment for parthenogenetic zooplankton, which allowed the upper limit of zooplankton establishment to be ground-truthed; however, three other α values were also incorporated. Values of $\alpha = 0.05$ and $\alpha = 0.001$ were also selected, representing 50% and 99% decreases in establishment probability from the initial value of 0.1 (Table 12). The lower α values represented less-invasive planktonic organisms (e.g., highly and moderately invasive plankton that are not parthenogenetic). To represent increases in establishment probability from the parthenogenetic zooplankton baseline, an α value of 0.9 was also chosen, reflecting the increased establishment potential for an invasive phytoplankton species. While the value of 0.9 is an approximation, it is widely regarded that the probability of phytoplankton to establish is much higher than for parthenogenetic zooplankton species (National Research Council 2011). For all establishment scenarios, Allee effects were assumed not to occur ($c = 1$). For the remainder of this document, categories of 'invasiveness' define differences in the ability of each functional group to establish at low population sizes (as determined by α values), rather than the ecological impact of the species following its establishment. For example, a zooplankton species with high 'invasiveness' has a higher probability of establishing at low population size than zooplankton with moderate invasiveness.

For comparison purposes, when α was 0.1, an initial population density of 100 individuals/m^3 would have a probability of establishing of $p = 0.9999$, while $\alpha = 0.001$ would lead to a much lower $P(E)$ of 0.095 (Figure 8).

Table 12. Establishment parameters for functional groups. Plankton parameters were ground-truthed through the mesocosm experiment from Bailey et al. (2009).

Description	Alpha Value in Risk-release Relationship	Rationale
Phytoplankton with high invasiveness	0.9	Best guess, based on expectations to establish at lower densities than a highly invasive parthenogenetic zooplankton species
Parthenogenetic zooplankton with high invasiveness	0.1	Empirical value derived from Bailey et al. 2009 mesocosm
Non-parthenogenetic zooplankton with high invasiveness	0.05	50% decrease in α from the parthenogenetic zooplankton value of 0.1

Description	Alpha Value in Risk-release Relationship	Rationale
Non-parthenogenetic zooplankton with moderate invasiveness	0.001	99% decrease in α from the parthenogenetic zooplankton value of 0.1
Adult molluscs with high invasiveness	0.1	Best guess, based on the potential reproductive capacity of transported organisms
Adult molluscs with moderate invasiveness	0.05	Best guess, based on the potential reproductive capacity of transported organisms
Macrophytes with high invasiveness	0.9	Best guess, based on the high establishment probability of single large (>35 g) plant fragments.

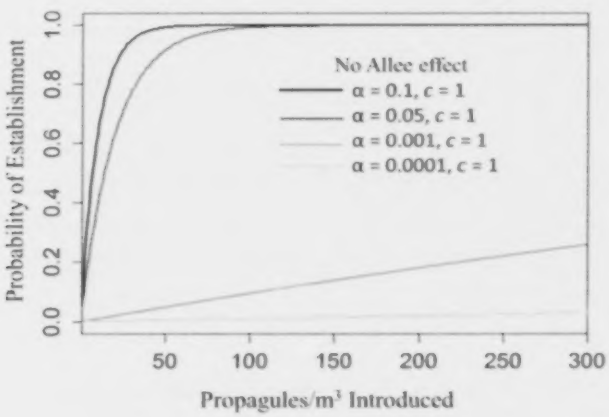


Figure 8. Demographic parameters leading to a given probability of establishment for the plankton functional group. The parameter α (alpha) describes the natural logarithm of the per-propagule probability of establishing and c = 1 signifies the lack of an Allee effect (Leung et al. 2004, National Research Council 2011). Reproduced from Drake et al. 2015b.

ESTIMATING THE OVERALL RATE OF BOATER-MEDIATED AIS SPREAD

Quantifying the overall rate of spread due to recreational boating involved:

i) simulating the invasion of a functional group at a single recreation access site;

ii) quantifying the infestation of boats operating in the vicinity of the site; and,

iii) determining, for each trip and yearly iteration of boating activity, which new recreational sites became invaded based on infested outbound, nearshore boater movements.

This approach allowed the secondary spread of each functional group to occur as a stepping-stone process (Floerl et al. 2009; Drake et al. 2015b), where new recreation sites beyond the original invaded source became sources themselves at time t+1 during subsequent years of boating. The model was developed as an agent-based process based on individual boating trips in the GLB, thereby allowing boats to interact with functional groups and create new founder populations across a ten year time horizon.

To conduct the simulation, a hypothetical species from each functional group (e.g., parthenogenetic zooplankton) was introduced to an individual recreational site. This inoculation can be thought of as a species introduced from a primary or secondary mechanism such as ballast, bait, overland recreational boating, or any other mechanism known to introduce AIS within the GLB. The introduced species was assigned a series of demographic parameters describing the change in population growth through time following the inoculation event, allowing population density (organisms/m^3 for plankton; organisms/m^2 for molluscs and macrophytes) at the recreation site to be estimated. To describe the change in population density through time, a logistic function of population growth was used as $F(x) = \frac{L}{1+e^{-k(x-x_0)}}$, where L is the maximum value of the logistic curve, k is the steepness of the curve, and x_0 is the time in years at which 50% of greatest population growth is reached. The value of L was set to the maximum reported density of each functional group known from the GLB. For example, for the parthenogenetic zooplankton group, L was set to an average maximum density of 37,200 organisms/m^3 and k was set to 1; see Appendix 2. For parthenogenetic zooplankton, x_0 was set to 1 (i.e., half of maximum population growth reached within 1 year following the initial introduction); whereas, for invasive phytoplankton, x_0 was set to 0.5, and for the least-invasive zooplankton scenario, x_0 was set to 5, representing 5 years for the population to reach half of maximum size (see Table 13 for demographic parameters). Population growth parameters were intentionally chosen to vary among functional groups, allowing the effect of different biological attributes on boater-mediated rates of spread to be quantified.

Quantifying the infestation of recreational boats with each functional group involved relating the in-water organism densities projected by the logistic function at time t to the densities hypothesized to be transported by each boat class, given the density of that functional group in the surrounding waterway. For the planktonic group, engine cooling water and livewell-type structures were known to contain organisms at densities generally consistent with densities found in surrounding surface waters. For example, mean zooplankton densities within livewells and engine cooling systems have been found to be consistent with expected densities of plankton within the surface waters of large freshwater lakes (Lake St. Clair: Johnson et al. [2001]; Lake Mead: Dalton and Cottrell [2013], Table 8). However, for the subset of boats lacking outboard motors or livewell-type intake structures, the density of organisms in standing water (i.e., accumulated water found in bilge areas) was considerably lower (e.g., a ten-fold reduction in density for standing water transported by boats; Johnson et al. 2001; Kelly et al. 2013).

To quantify the degree of infestation of each functional group, each trip was assigned a boat classification based on the proportion of trips occurring for each boat type (e.g., power-driven, sail-driven, and manually-driven). Additional trip characteristics were assigned based on the Ontario survey data such as the prevalence of in-water boat storage, which would also lead to differences in infestation among trips for organisms with direct attachment potential and for transported macrophytes. For example, manually-driven boats would be unlikely to have structures such as livewells, so maximum densities transported by that boat class would be reduced compared to the density of organisms in surrounding surface waters.

Table 13. Population parameters of functional groups.

Functional Group	α, natural logarithm of the per-propagule probability of establishing	X_o (time in years to reach half of maximum population density in waters surrounding recreation site)	L_{max} (estimated average maximum population density in GLB, m^2 or m^3)
Phytoplankton with high invasiveness	0.9	0.5	43,400 cells/m^3
Parthenogenetic zooplankton with high invasiveness	0.1	1	37,700 organisms/m^3
Non-parthenogenetic zooplankton, high invasiveness	0.05	2	31,000 organisms/m^3
Non-parthenogenetic zooplankton, moderate invasiveness	0.001	5	24,800 organisms/m^3
Molluscs with high invasiveness (e.g., Zebra Mussel)	0.1	2	20,000 adults/m^2
Molluscs with moderate invasiveness (e.g., New Zealand Mud Snail)	0.05	5	5,600 adults/m^2
Macrophytes with high invasiveness	0.9	5	300 stems/m^2

Each of the 1,717 recreational access points were sequentially inoculated with a functional group. For the number of yearly trips leaving the inoculated access point (number of trips drawn from the negative binomial trip distribution), each trip was categorized as a power-driven boat (81.8% of trips), sail-driven boat (4.3% of trips), or manually-operated boat (13.9% of trips). For power-driven boats, the infestation density of each trip was based on a Poisson distribution, with lambda (λ) equal to the in-water density predicted by the logistic function at time *t*. This reflected the maximum density of propagules transported in engine cooling systems or livewell type structures. Sail-powered boats had λ times 0.5, reflecting an assumed decrease in propagule density due to less-frequent outboard motor use. Manually-powered boats had λ times 0.1, reflecting strong reductions in the density of organisms contained within standing water based on Kelly et al. (2013). While boat structures other than engine cooling water, livewell-type structures, or standing water could be infested, the chosen structures and densities were those known to support maximum propagule concentrations and thus provide the likely maximum density and highest probability of establishment for a given trip.

Following the infestation of a single outbound trip at a predetermined density, the spatial distribution of the trip was projected. A Bernoulli trial was conducted where the probability of undertaking an offshore trip was equal to the probability of undertaking a nearshore trip ($p = 0.5$ for each scenario). For nearshore trips, the maximum Euclidean on-water travel distance (km) was randomly selected from the log-normal dispersal kernel. For each randomly selected travel distance, the recreational sites available within the nearshore search radius were identified, representing the set of possible nearshore sites that could be visited by the infested boat. The nearshore site that was located at the greatest on-water distance from the original invaded

location but within the trip's nearshore search radius was selected for visitation, and a uniform probability of 0.5 was incorporated to reflect the probability that the boat released its propagules during the visit to this new recreational site. While this probability of release is inevitably an overestimate (and represents a best guess), detailed data were unavailable to describe release timing. With this overestimate of release and the forced behaviour of a boater to select the new recreational site at greatest on-water distance from the source location, the spread model provided a 'worst-case' estimate (i.e., greatest geographic extent) under a series of simplifying conditions.

Following the release of propagules during the visit to the new recreational site, the density released by each boat was multiplied by a random value between 0.1 and 0.99, reflecting the change in organism density following physical dispersion within the water column (i.e., most organisms physically disperse following their release). The resulting change in density was then evaluated against the probability of establishment relationship from Leung et al. (2004), where $PE(N_t) = 1 - e^{-(\alpha N t)^{\wedge} c}$, with $P(E)$ as the probability that released organisms will establish a viable population, N_t is the released population density (propagules/m^3), α is the natural logarithm of the per-propagule probability of establishing (a mathematical parameter defined based on the mesocosm experiment from Bailey et al. [2009]), and c was set equal to 1. A random value between 0 and 1 was evaluated against the per-trip probability of establishment, where a trip resulted in invasion (random value < $P(E)$) or failure (random value > $P(E)$).

The remaining n trips leaving the invaded source were evaluated using the same probabilistic framework, leading to n new invaded recreational sites in year 1 from the single invaded source. The success (invasion) or failure (lack of invasion) at each new recreational site was recorded at the end of the yearly iteration of boating activity, which represented a single yearly iteration of the model.

The invaded sites at the end of year 1 represented invaded satellite populations. These new source locations became potential sources themselves for propagules to be taken up during year 2, but with reduced population densities (and a similarly reduced probability of uptake) in new locations based on the single year of population growth. The yearly progression of boater trips and the invasion of new sites continued across a ten year period, providing a ten-year window of recreation site invasion in the GLB resulting from a single 'seeded' source location. An example of the progression of satellite population development is shown in Figure 9. Variation in spread through the 10 year period was evaluated by simulating 10 iterations of each ten year run (i.e., 10 years times 10 trials) for each of 1,717 recreational access points.

Results of boater-mediated spread timelines are shown for phytoplankton, parthenogenetic zooplankton, non-parthenogenetic zooplankton (high invasiveness, moderate invasiveness), molluscs (high invasiveness, moderate invasiveness), and macrophytes, which describe the mean time for an inoculated functional group to spread from origin to destination lake in the GLB based on recreational boating activity (Tables 14 through 20, respectively; invasiveness categories based on population growth parameters). The probability distributions of lake-to-lake boater-mediated spread timelines that illustrate variation around these mean values are shown in Appendix 3.

Two broad conclusions exist about boater-mediated spread timelines. First, because the longest boating trips were also the rarest, the furthest lake-to-lake connections generally took the longest to become invaded (e.g., St. Lawrence to Superior, Michigan to St. Lawrence). However, boater-mediated invasion along these routes did occur with sufficient time, leading to the development of 'new' pathways of AIS introduction (e.g., St. Lawrence to Superior, mean of 8 years for boater-mediated spread of invasive phytoplankton, Erie to Superior, mean of 9.5 years for moderately invasive molluscs). Second, there were notable increases in the time

required for species to invade as demographic parameters were decreased. For example, the boater-mediated spread of invasive phytoplankton from Lake Erie to Lake Huron would take an average of 5.15 years; whereas, the spread of moderately invasive zooplankton would take roughly three years longer (8.87 years). The relationship between demographic rates and spread timeframe exists because as demographic rates decrease, a greater proportion of infested trips result in failed invasion because of lower reproductive potential. These findings indicate that boater-mediated spread in the GLB is influenced by the interaction between boating activity and the demographic characteristics of transported AIS.

Table 14. Mean boater-mediated spread timelines for the phytoplankton functional group. Values represent the mean time from inoculation at a recreational access site in an origin lake (vertical axis) to the establishment of at least one satellite population at a destination lake (horizontal axis). Values within cells represent mean time in years. An X indicates that within-lake spread was not recorded, while NA indicates that the majority of iterations had timeframes that were longer than the modeled 10 year window.

	Superior	Michigan	Huron	Erie	Ontario	St. Lawrence
Superior	X	5.07	4.07	8.79	8.13	8.9
Michigan	3.7	X	2.74	5.1	8.6	NA
Huron	3.1	2.3	X	4.8	6.2	7.5
Erie	8.03	6.59	5.15	X	3.38	5.62
Ontario	7.91	8.74	5.24	2.38	X	2.6
St. Lawrence	8.0	NA	5.0	2.6	1.0	X

Table 15. Mean boater-mediated spread timelines for the parthenogenetic zooplankton functional group. Values represent the mean time from inoculation at a recreational access site in an origin lake (vertical axis) to the establishment of at least one satellite population at a destination lake (horizontal axis). Values within cells represent mean time in years. An X indicates that within-lake spread was not recorded, while NA indicates that the majority of iterations had timeframes that were longer than the modeled 10 year window.

	Superior	Michigan	Huron	Erie	Ontario	St. Lawrence
Superior	X	6.5	3.65	8.86	9.66	NA
Michigan	4.1	X	2.6	6.5	8.7	NA
Huron	3.3	2.7	X	6.47	8.38	9.47
Erie	7.64	6.19	5.13	X	3.48	5.41
Ontario	9.66	9.18	8.16	2.47	X	2.56
St. Lawrence	NA	NA	8	4	1	X

Table 16. Mean boater-mediated spread timelines for the non-parthenogenetic zooplankton group (high invasiveness). Values represent the mean time from inoculation at a recreational access site in an origin lake (vertical axis) to the establishment of at least one satellite population at a destination lake (horizontal axis). Values within cells represent mean time in years. An X indicates that within-lake spread was not recorded, while NA indicates that the majority of iterations had timeframes that were longer than the modeled 10 year window.

	Superior	Michigan	Huron	Erie	Ontario	St. Lawrence
Superior	X	5.32	3.55	8.55	8.64	9
Michigan	4.2	X	2.88	7.48	9.53	NA
Huron	3.42	2.76	X	6.06	8.14	9.33
Erie	8.95	NA	6.01	X	3.51	5.5
Ontario	8.38	NA	6.13	2.42	X	2.43
St. Lawrence	10	NA	6	3.66	1	X

Table 17. Mean boater-mediated spread timelines for the non-parthenogenetic zooplankton functional group (moderate invasiveness). Values represent the mean time from inoculation at a recreational access site in an origin lake (vertical axis) to the establishment of at least one satellite population at a destination lake (horizontal axis). Values within cells represent mean time in years. An X indicates that within-lake spread was not recorded, while NA indicates that the majority of iterations had timeframes that were longer than the modeled 10 year window.

	Superior	Michigan	Huron	Erie	Ontario	St. Lawrence
Superior	X	8.57	5.9	NA	NA	NA
Michigan	7.39	X	5.22	NA	NA	NA
Huron	5.55	3.95	X	NA	NA	NA
Erie	NA	NA	8.87	X	6.59	8.74
Ontario	9.64	NA	6.26	4.08	X	3.82
St. Lawrence	NA	NA	8	6.33	1.6	X

Table 18. Mean boater-mediated spread timelines for the mollusc functional group (high invasiveness). Values represent the mean time from inoculation at a recreational access site in an origin lake (vertical axis) to the establishment of at least one satellite population at a destination lake (horizontal axis). Values within cells represent mean time in years. An X indicates that within-lake spread was not recorded, while NA indicates that the majority of iterations had timeframes that were longer than the modeled 10 year window.

	Superior	Michigan	Huron	Erie	Ontario	St. Lawrence
Superior	X	7.71	5.48	NA	NA	NA
Michigan	7.14	X	4.94	NA	NA	NA
Huron	4.72	6.49	X	NA	NA	NA
Erie	NA	NA	NA	X	4.75	8.66
Ontario	NA	NA	NA	3.45	X	3.94
St. Lawrence	NA	NA	NA	8	3	X

Table 19. Mean boater-mediated spread timelines for the mollusc functional group (moderate invasiveness). Values represent the mean time from inoculation at a recreational access site in an origin lake (vertical axis) to the establishment of at least one satellite population at a destination lake (horizontal axis). Values within cells represent mean time in years. An X indicates that within-lake spread was not recorded, while NA indicates that the majority of iterations had timeframes that were longer than the modeled 10 year window.

	Superior	Michigan	Huron	Erie	Ontario	St. Lawrence
Superior	X	7.91	6.44	NA	NA	NA
Michigan	7.73	X	4.3	NA	NA	NA
Huron	5.2	5	X	NA	NA	NA
Erie	9.5	8.82	7.42	X	5.01	8.82
Ontario	NA	10	9.4	4.15	X	3.78
St. Lawrence	NA	NA	NA	6.5	2	X

Table 20. Mean boater-mediated spread timelines for the macrophyte functional group. Values represent the mean time from inoculation at a recreational access site in an origin lake (vertical axis) to the establishment of at least one satellite population at a destination lake (horizontal axis). Values within cells represent mean time in years. An X indicates that within-lake spread was not recorded, while NA indicates that the majority of iterations had timeframes that were longer than the modeled 10 year window.

	Superior	Michigan	Huron	Erie	Ontario	St. Lawrence
Superior	X	7.74	6.29	NA	NA	NA
Michigan	7.85	X	4.2	NA	NA	NA
Huron	5.18	5.03	X	NA	NA	NA
Erie	9.5	9.02	7.58	X	4.87	8.77
Ontario	NA	NA	9.68	4.19	X	3.92
St. Lawrence	NA	NA	10	5.5	1	X

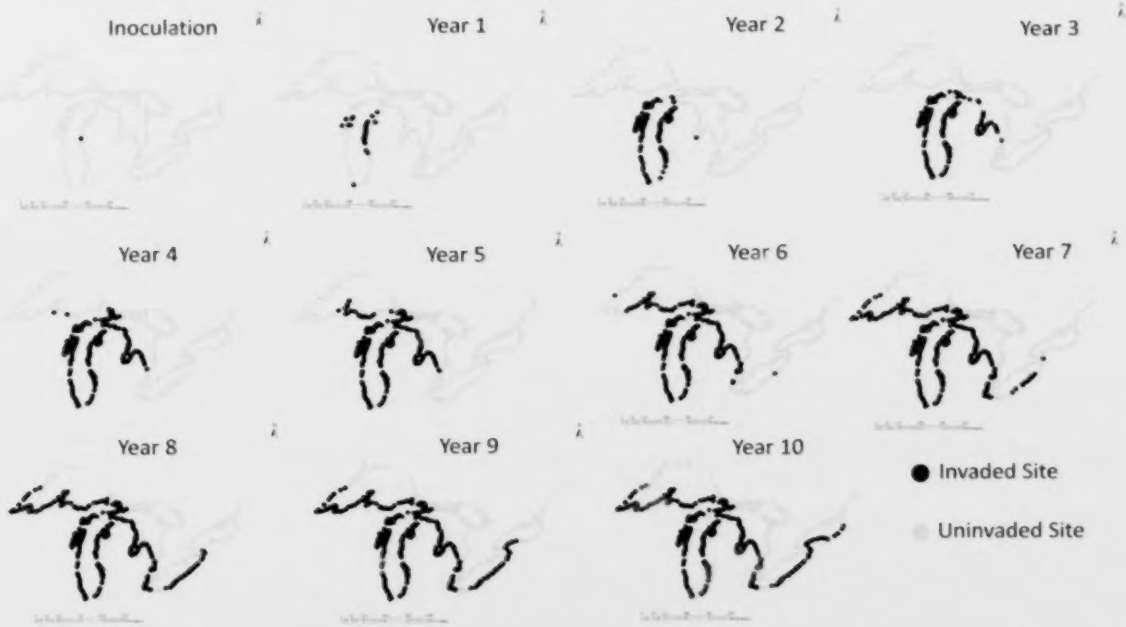


Figure 9. Example of a ten-year iteration of the boater-mediated spread of parthenogenetic zooplankton introduced to a recreational site in Lake Michigan near Manistee, MI.

OVERALL ESTIMATE OF THE ECOLOGICAL RISK OF RECREATIONAL BOATING AS A PATHWAY FOR THE SECONDARY SPREAD OF AIS IN THE GLB

Estimating the ecological risk of recreational boating within the GLB was evaluated by comparing the rate of boater-mediated AIS spread (see Tables 14–20 and Appendix 3 for lake-to-lake timelines) against the time required for AIS to disperse naturally, where the quickening of spread due to boating, relative to a natural dispersal baseline, was of interest This approach recognizes that a faster rate of AIS spread due to boating increases the occupancy of a species per unit time, thus increasing the rate at which ecological (and socioeconomic) impacts occur. In some cases, boater-mediated upstream movements signify the development of new pathways of AIS dispersal that may otherwise be extremely unlikely to occur over short (~10 year) timescales, allowing AIS access to ecosystems that were previously unavailable.

To quantify the change in spread relative to natural dispersal, a directional lake-to-lake natural dispersal matrix was created where origin lakes were listed on the vertical axis, and destination lakes were listed on the horizontal axis (Table 21). Origin lakes indicate the location where natural dispersal of newly introduced AIS begins, and destination lakes are those where natural dispersal terminates (or passes through), and must include the establishment of at least one satellite population. Values within cells of the matrix represent the estimated timeline for natural dispersal between each pairwise combination of lakes. The estimate of natural dispersal was generic across functional groups, given the lack of reliable data describing organism movement in the absence of human vectors. However, most functional groups modelled are relatively sessile, likely undergoing the greatest degree of transport during the larval or planktonic stage. Mechanistic models describing the probability of organisms with larval life stages dispersing within the GLB have recently been developed. For example, Beletsky et al. (2007) determined that larval fishes typically require 2–3 months to traverse between southwestern Lake Michigan and Grand Traverse Bay, with seasonal patterns of movement based on wind driven changes in water flow. Other models (Beletsky et al. 2017) indicate that rates of natural dispersal are highly dependent on the location of introduction and the life history characteristics of target organism, and also vary substantially between years due to the inter-annual variation in lake currents. Given these findings, movement within a lake is likely highly variable, but may occur relatively quickly, compared with upstream movements between lakes, which are likely slower due to the presence of physical barriers (e.g., locks) and the need to overcome higher water velocities in connecting channels.

The following rules were derived to estimate rates of natural dispersal, assuming a worst-case (i.e., fastest) scenario, based largely on extrapolating from Beletsky et al. (2007). Organisms were assumed to travel within a lake basin within a single year following an inoculation event. Downstream movements to reach another lake were assumed to add an additional year of travel time (e.g., an organism would require an average of two years to transit between Lake Huron and Lake Erie). Upstream movements via natural dispersal were assumed to not occur over the 10 year study period. Exceptions for this rule involved:

1) dispersal from Lake Huron to Lake Michigan, due to variable flow and discharge rates in the Straits of Mackinac, where upstream movement into Lake Michigan could occur within five years; and,

2) outbound from Lake Superior where, due to its size, two years in total would be required, on average, for dispersing organisms to reach Sault Ste. Marie, resulting in three years of outbound dispersal to Lake Huron and Lake Michigan.

Because the natural dispersal estimates are extremely uncertain and measured at such a coarse level, the effect of the chosen natural dispersal values was quantified through sensitivity

analysis. Two scenarios were incorporated where natural dispersal rates were lengthened over baseline, representing a doubling and quadrupling of the time it takes an organism to disperse naturally among lake basins. These scenarios were designed to reflect scenarios in which the baseline estimates of natural dispersal have overestimated the speed at which natural dispersal occurs. In addition, a negative binomial natural dispersal matrix was also incorporated to determine if more variable estimates of natural dispersal would influence on model results. The final 'fixed' natural dispersal matrix is given in Table 21.

Table 21. Estimates of the timeline (values in years) of natural dispersal for introduced AIS between origin lakes (vertical axis of table) and destination lakes (horizontal axis of table). Values are generic across functional groups and represent an estimate of the time required for a sessile species to transit between each lake ecosystem. A value of >10 years indicates that it is extremely unlikely for a sessile organism to disperse naturally over the course of the modeled ten-year period.

		Destination Lake					
		St. Lawrence	**Ontario**	**Erie**	**Huron**	**Michigan**	**Superior**
Origin Lake	**Superior**	6	5	4	3	3	X
	Michigan	5	4	3	2	X	>10
	Huron	4	3	2	X	5	>10
	Erie	3	2	X	>10	>10	>10
	Ontario	2	X	>10	>10	>10	>10
	St. Lawrence	X	>10	>10	>10	>10	>10

The natural dispersal matrix was evaluated against the boater-mediated spread matrix derived for each functional group (Tables 14–20). Because the boater-mediated spread matrix was composed of multiple ten-year iterations of boating activity, each of 10 individual outcomes of spread were recorded for each of 1,717 inoculation events. Therefore, each 'cell' of the boater-mediated spread matrix between origin lake *i*, and destination lake *j*, is a probability distribution function of possible *ij* timelines (Appendix 3). The variation around boater-mediated spread estimates was a function of stochasticity of the modelled biological parameters, plus stochastic uncertainty in the number of boater-mediated events leaving a given recreational access point, as well as the differences in the boater-mediated rate of lake-to-lake spread when different recreational access sites within a lake are invaded (e.g., central basin ports vs 'fringe' ports near connecting channels). The change in natural dispersal relative to boater-mediated spread was calculated as: [boater-mediated dispersal timeline, *ij*] – [natural dispersal timeline, *ij*], which in some cases produced a negative value (considered as the quickening of spread attributed to recreational boating) used to assign the consequence categories listed in Table 2. This approach allowed the variation in natural dispersal timelines to be carried over to consequence categories. The resulting probability distribution function of impact categories (i.e., the risk distribution; see Figure 10 for examples) describes the probability that a given consequence will occur, given stochastic uncertainty within the model. Consequence categories were 'Very Low Consequence' (boater-mediated rate of spread that is slower than, equal to, or only marginally faster than natural dispersal [< 1 year]), Low Consequence (boating activity leads to spread that is 1 or 2 years faster than natural dispersal), Moderate Consequence (boating activity leads to spread that is 3 or 4 years faster than natural dispersal), High Consequence (boating activity leads to spread that is 5 years faster than natural dispersal), and Very High Consequence (boating activity leads to spread that is more than 5 years faster than natural dispersal,

signifying that boater-mediated spread has occurred in an upstream direction, leading to a new pathway of AIS dispersal).

Risk distributions were calculated at the receiving lake level to understand the overall consequence of spread if the identity of the origin lake or inoculation site was unknown (Figure 10; can also be considered as the consequence if all lakes other than recipient have contributed equally as sources). For example, Lake Superior is Likely to experience a Very High ecological consequence when invasive phytoplankton is inoculated anywhere within the GLB other than Lake Superior, because phytoplankton would be unlikely to naturally colonize Lake Superior within the ten-year window and the majority of ten-year iterations involved boater-mediated upstream dispersal to Lake Superior. However, in some cases, boater-mediated phytoplankton failed to reach Lake Superior, which is seen as the Low likelihood of a Very Low consequence (left bar of upper left graph in Figure 10).

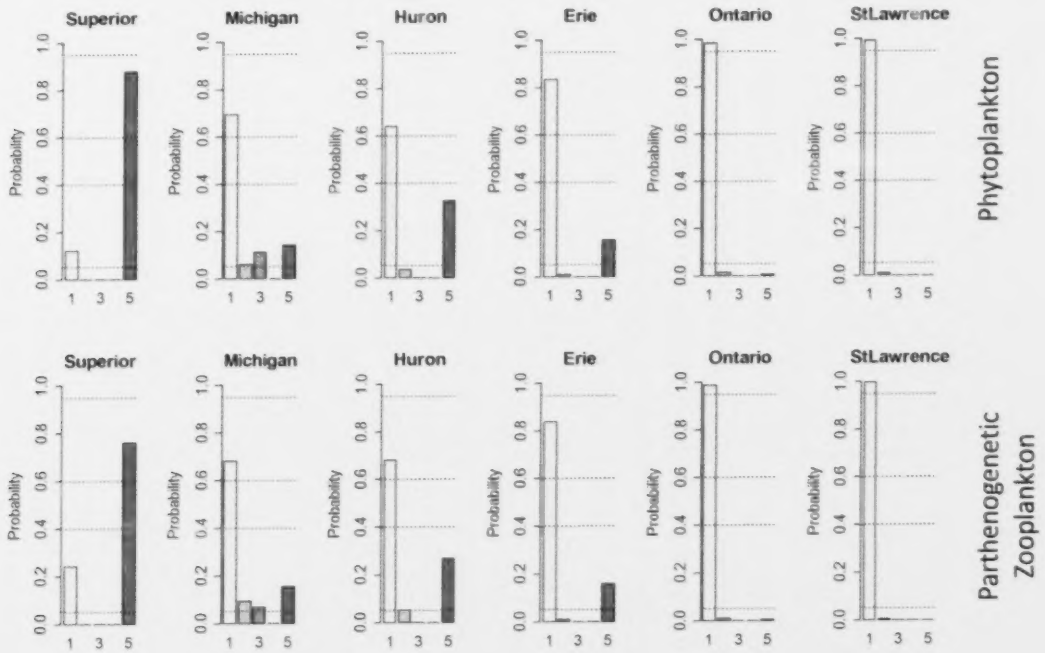


Figure 10. Summary of ecological risk across functional groups of AIS (group label shown at right of vertical axis) and aggregated at recipient lakes in the Great Lakes basin. ***The x-axes are consequence categories.*** *Figure panels represent the difference in boater-mediated spread timeline relative to natural dispersal, based on consequence categories in Table 2. Horizontal dotted lines show the boundaries of likelihood categories. Each figure cell describes the probability of each consequence category occurring. For example, in the upper left, a very high ecological impact to Lake Superior is expected to occur with high likelihood following the inoculation of invasive phytoplankton in the Great Lakes basin, while a very low ecological impact is expected to occur with low likelihood. Consequence category '5' (dark red bars) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is 1717 (reflecting 1717 access points), minus the number of access points within the lake of interest (within-lake spread removed), with each datapoint representing a ten-year iteration of boating activity.*

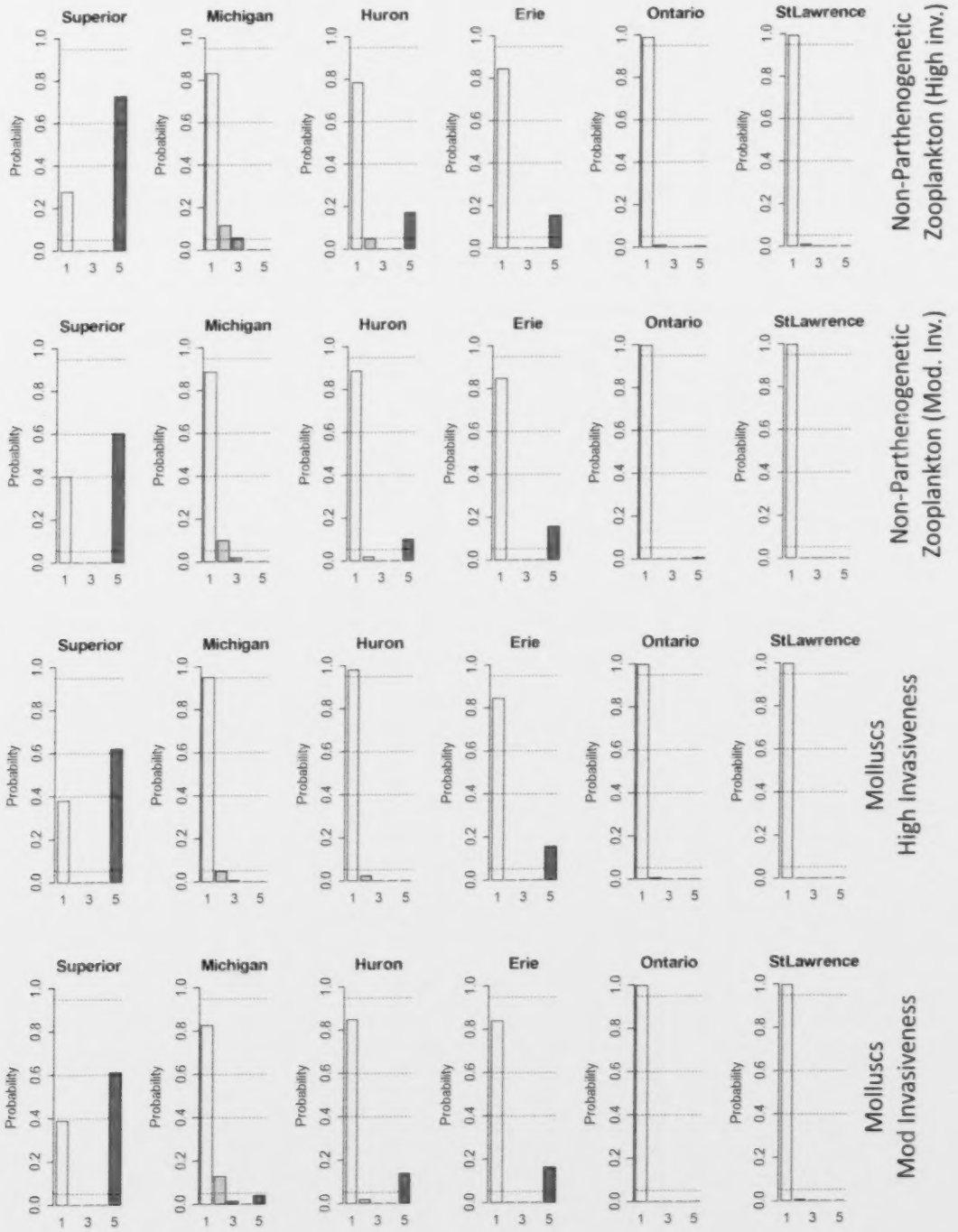


Figure 10. Continued.

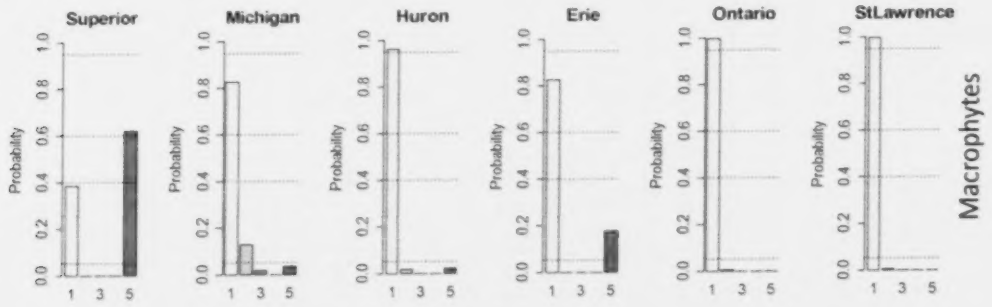


Figure 10. Continued.

In contrast, the most likely consequences to Lake Michigan, Lake Huron, Lake Erie, Lake Ontario, and the St. Lawrence River were Very Low, though each waterbody can experience strong changes in baseline spread due to boater-mediated movement of AIS, especially those with multiple connections from downstream sources like Lake Michigan, Lake Huron, and Lake Erie. Lake Michigan, Lake Huron, Lake Erie, Lake Ontario, and the St. Lawrence River could receive downstream movements that circumvented the rate of natural dispersal by up to 4 years, but these usually occur with either Low or Very Low likelihood.

Risk distributions were also summarized at the *ij*, lake-to-lake level, allowing the risk of secondary spread to and from individual lakes to be better understood when the lake experiencing the inoculation event is known (Figures 11 through 17). For example, Figure 11 describes the ecological risk of secondary spread between lakes for invasive phytoplankton. When Lake Superior has been inoculated, the most likely consequence to all receiving lakes is Low, signifying that boater-mediated spread is generally occurring at a rate that is consistent with or slower than natural dispersal, though in some cases the rate of boater-mediated spread is faster than natural dispersal when considering movement to Lake Huron. In contrast, when the St. Lawrence River has been inoculated, the most likely consequence for most receiving lakes is Very High, signifying that boater-mediated spread has occurred within a ten-year period, leading to new upstream pathways of AIS dispersal. In general and across most lake-to-lake pairings, there was a relatively poor ability of boating activity to establish populations at downstream sources at rates quicker than natural dispersal, while the development of new upstream pathways of dispersal was far more likely. The overall estimate of certainty within the model ranged from High, such as when the negative binomial natural dispersal matrix was incorporated or when model parameters were reduced by 25%, to Low, such as when natural dispersal timelines were lengthened (quadrupled), leading to substantial changes in consequence categories (Figure 18).

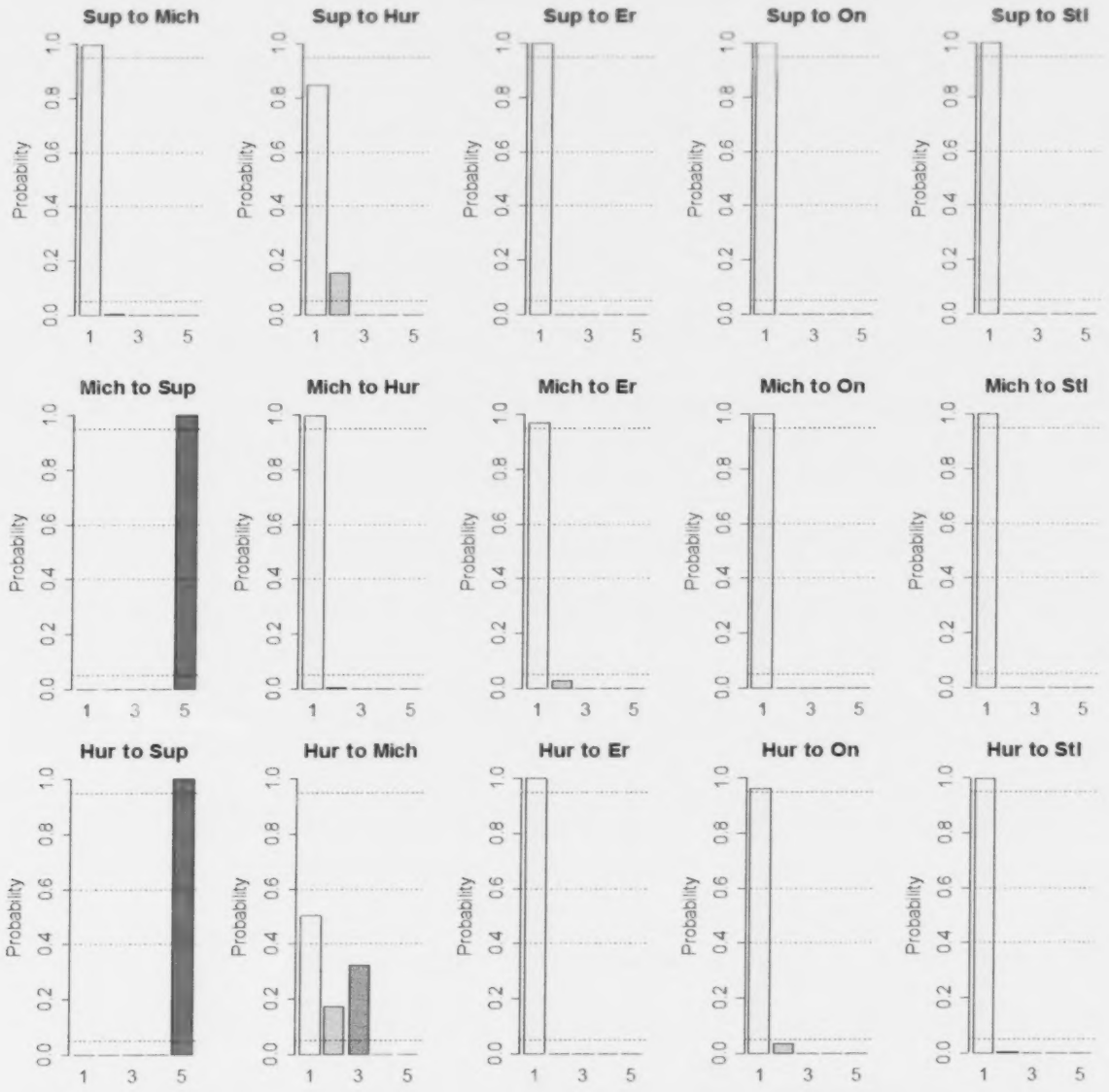
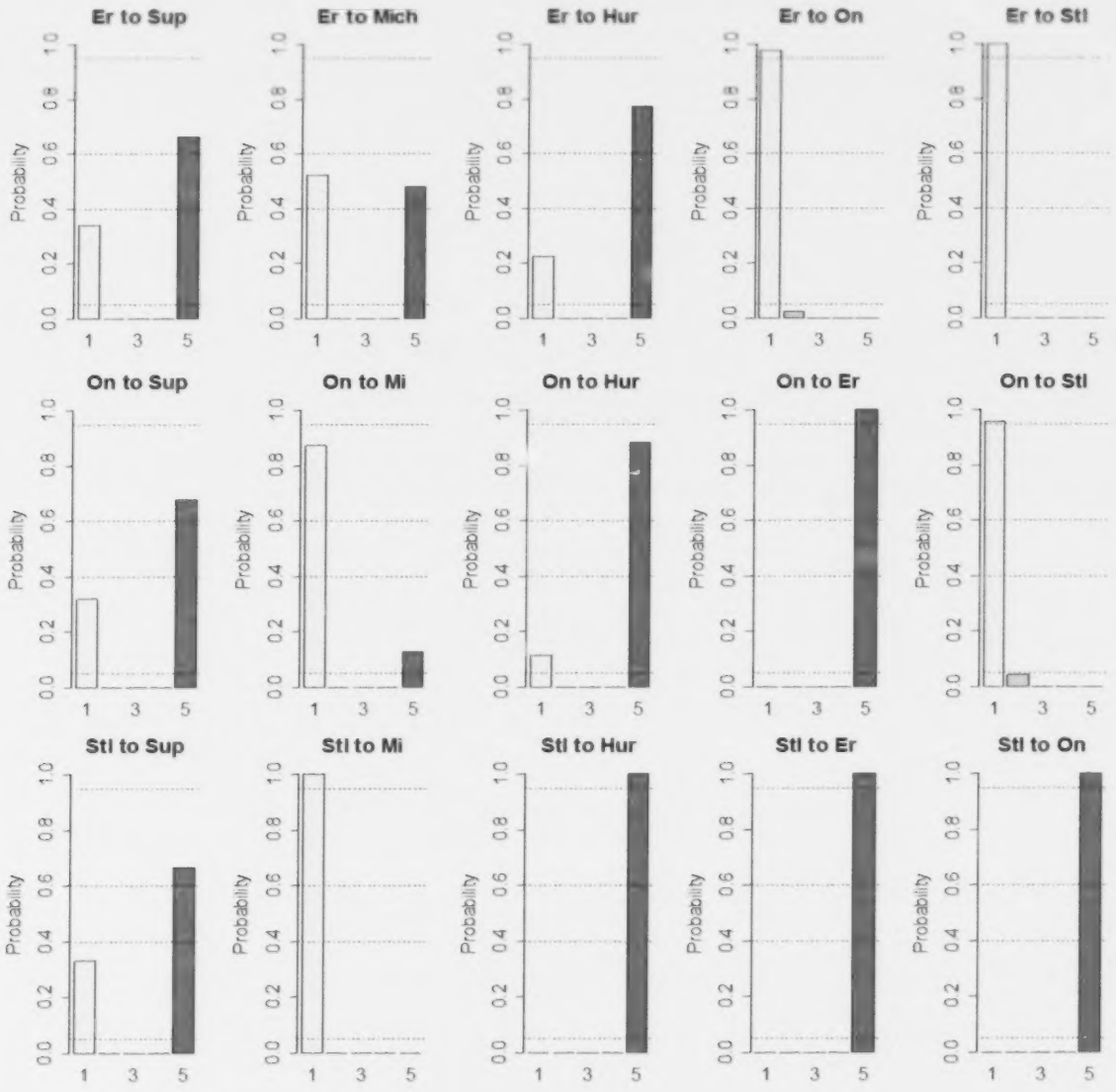


Figure 11. Ecological risk of lake to lake secondary spread of invasive phytoplankton due to recreational boating in the GLB. ***The x-axes are consequence categories.*** *Figure panels represent the change in boater-mediated secondary spread relative to natural dispersal (see Table 2 for consequence categories). Lake to lake spread is labelled at the top of each graph (e.g., upper left shows spread from an inoculation in Lake Superior to Lake Michigan). Dotted horizontal lines represent the boundaries of likelihood categories. Consequence category '5' (dark red bar) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is equal to the number of access points (and inoculation events) in each origin lake.*



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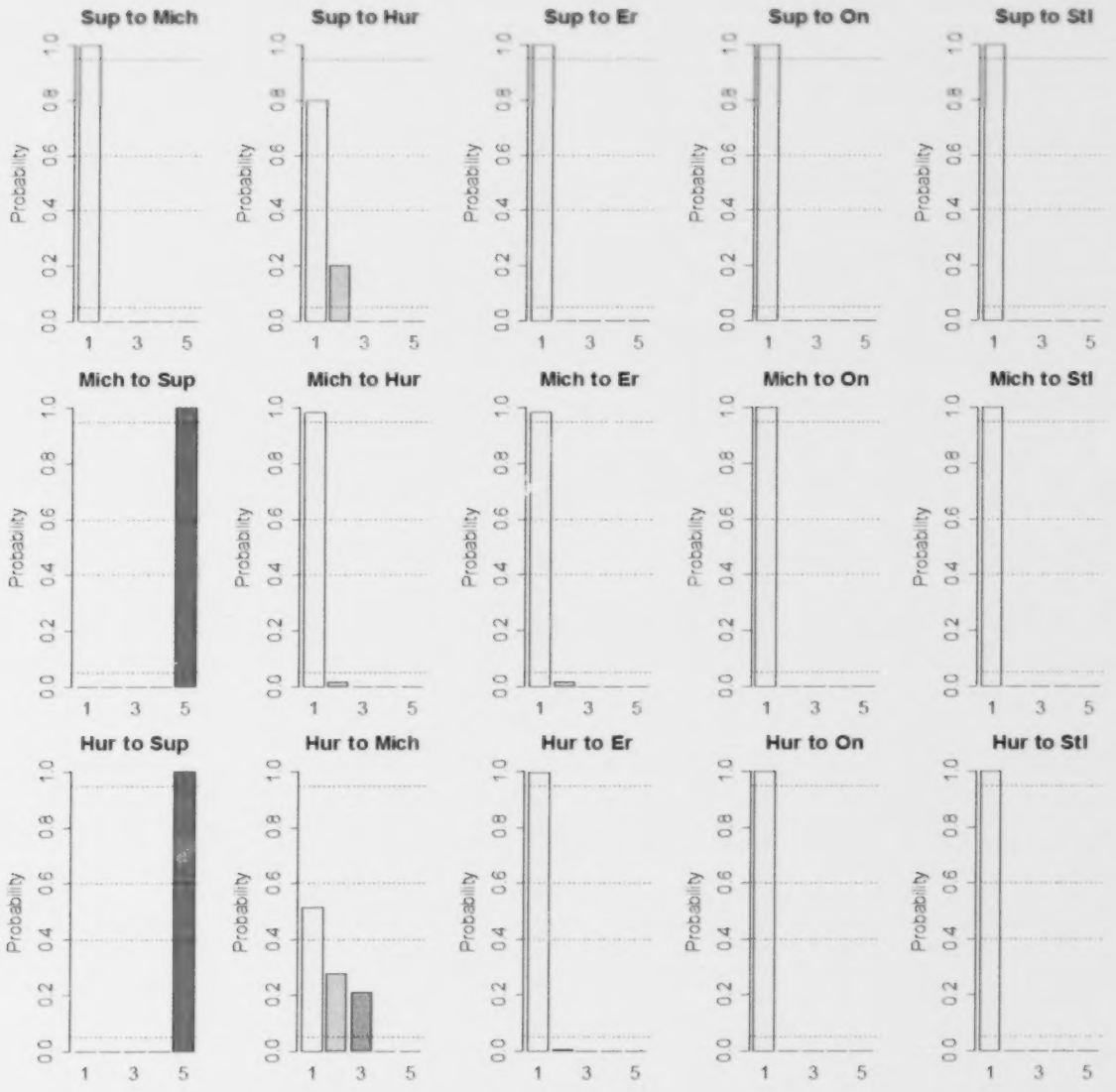
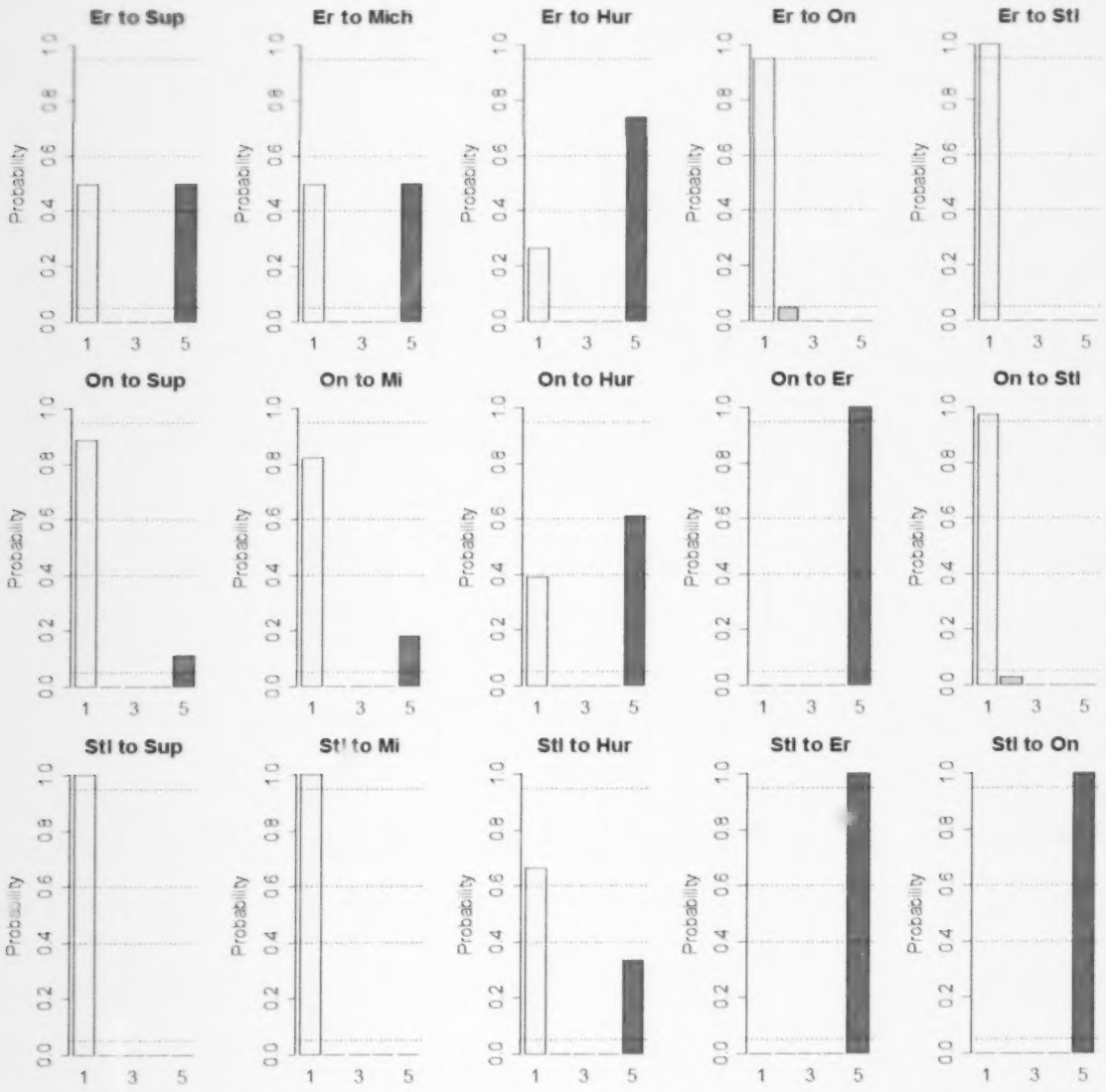


Figure 12. Ecological risk of lake to lake secondary spread of parthenogenetic zooplankton due to recreational boating activity in the GLB. ***The x-axes are consequence categories.*** *Figures display the change in boater-mediated secondary spread relative to natural dispersal (see Figure 1 and Table 2 for consequence categories). Lake to lake spread is labelled at the top of each graph (e.g., upper left shows spread from an inoculation in Lake Superior to Lake Michigan). Dotted horizontal lines represent the boundaries of likelihood categories. Consequence category '5' (dark red bars) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is equal to the number of access points (and inoculation events) in each origin lake.*



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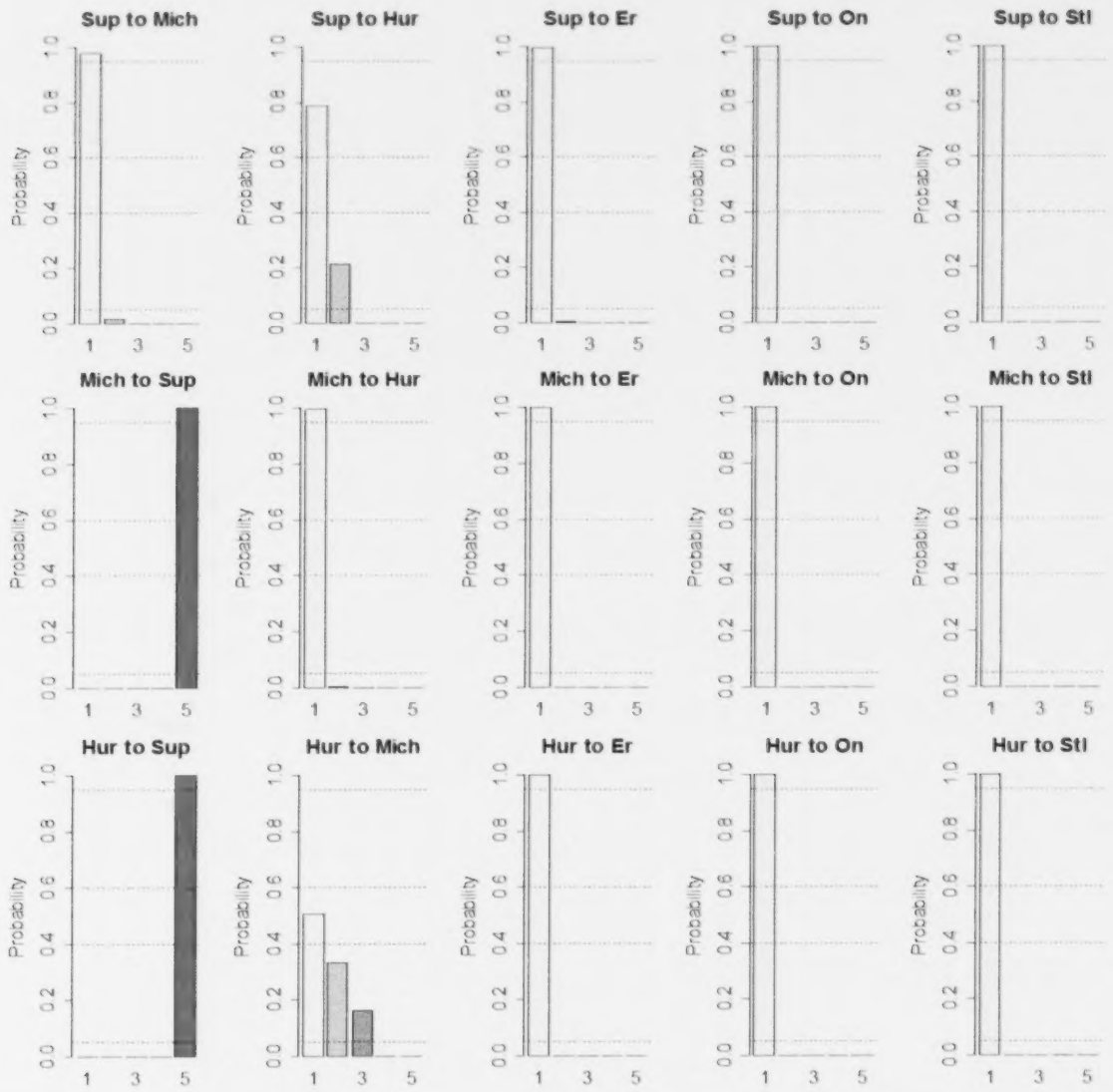
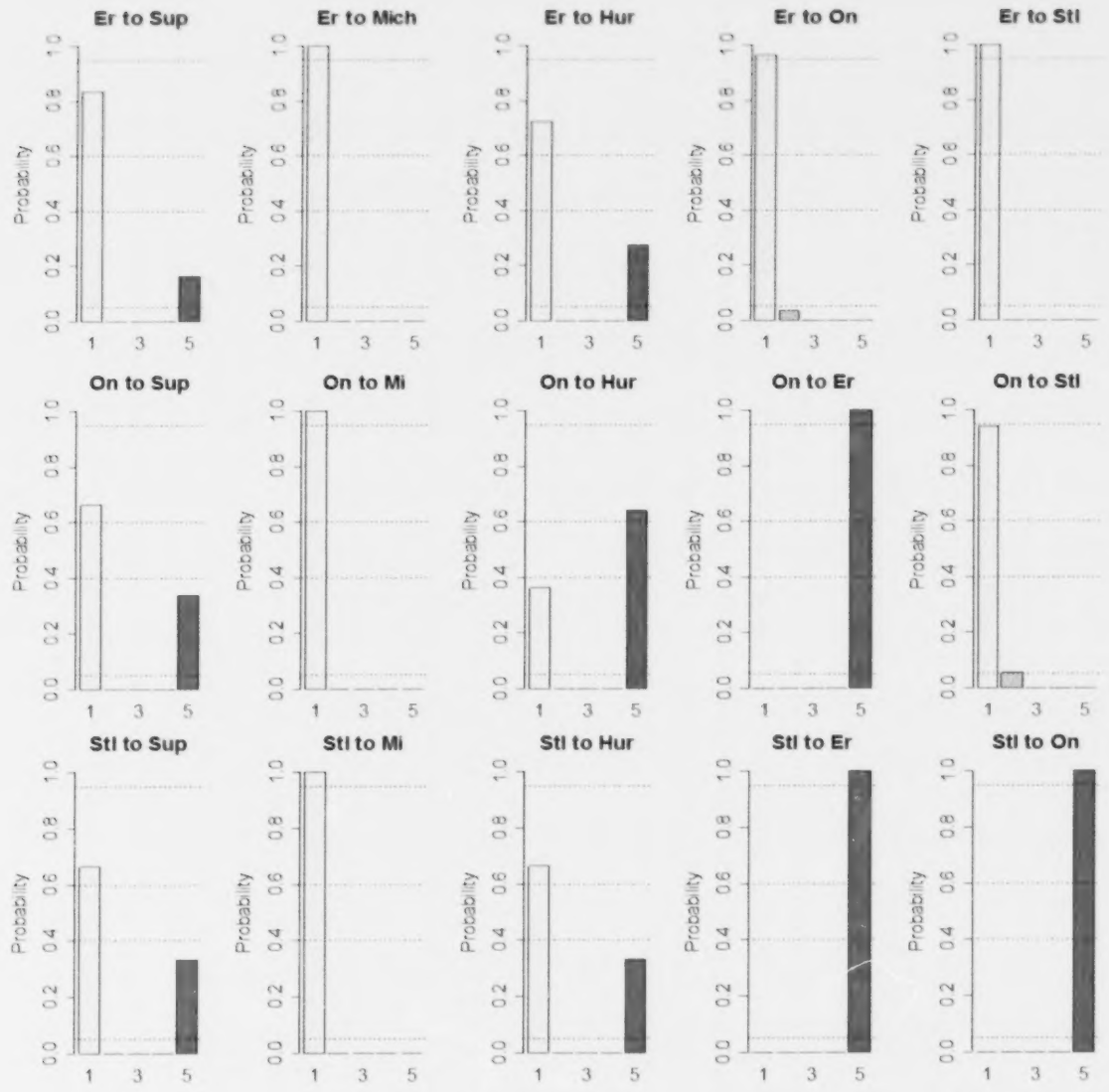


Figure 13. Ecological risk of lake to lake secondary spread of non-parthenogenetic zooplankton (high invasiveness) due to recreational boating activity in the GLB. ***The x-axes are consequence categories.*** *Figure panels represent the change in boater-mediated secondary spread relative to natural dispersal (see Figure 1 and Table 2 for consequence categories). Lake to lake spread is labelled at the top of each graph (e.g., upper left shows spread from an inoculation in Lake Superior to Lake Michigan). Dotted horizontal lines represent the boundaries of likelihood categories. Consequence category '5' (dark red bars) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is equal to the number of access points (and inoculation events) in each origin lake.*



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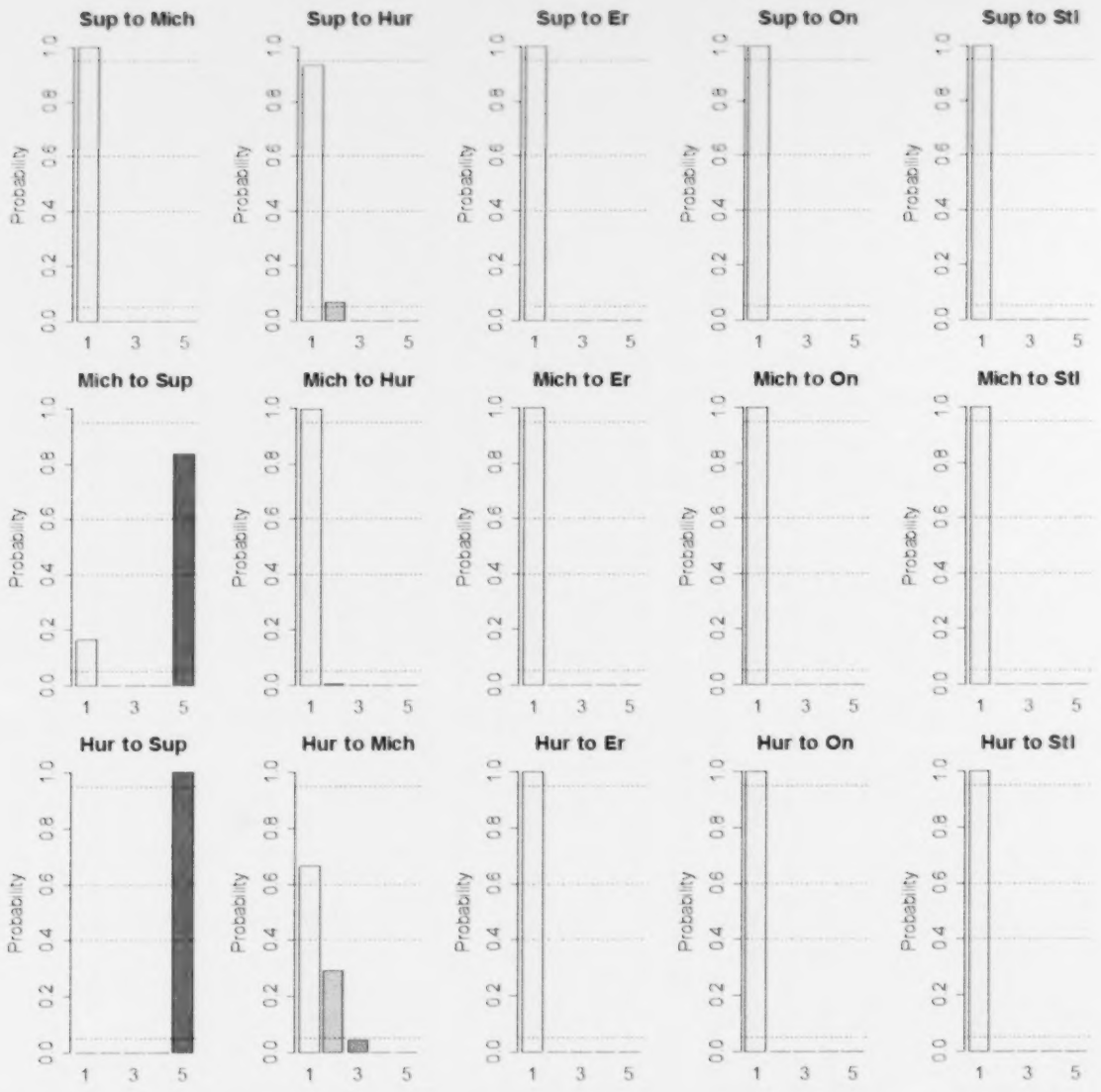
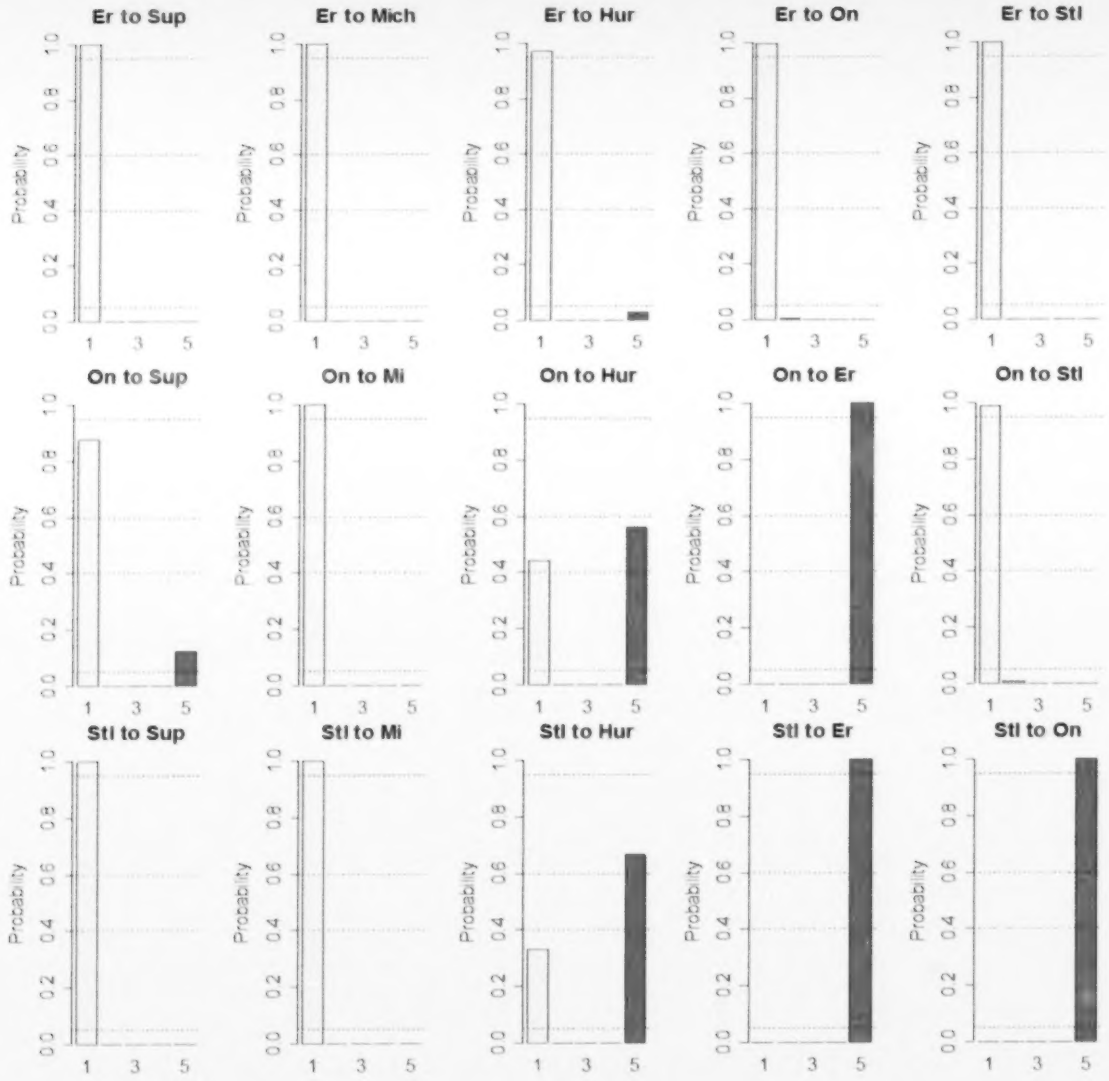


Figure 14. Ecological risk of lake to lake secondary spread of non-parthenogenetic zooplankton (moderate invasiveness) due to recreational boating activity in the GLB. ***The x-axes are consequence categories.*** *Figure panels represent the change in boater-mediated secondary spread relative to natural dispersal (see Figure 1 and Table 2 for consequence categories). Lake to lake spread is labelled at the top of each graph (e.g., upper left shows spread from an inoculation in Lake Superior to Lake Michigan).Dotted horizontal lines represent the boundaries of likelihood categories. Consequence category '5' (dark red bars) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is equal to the number of access points (and inoculation events) in each origin lake.*



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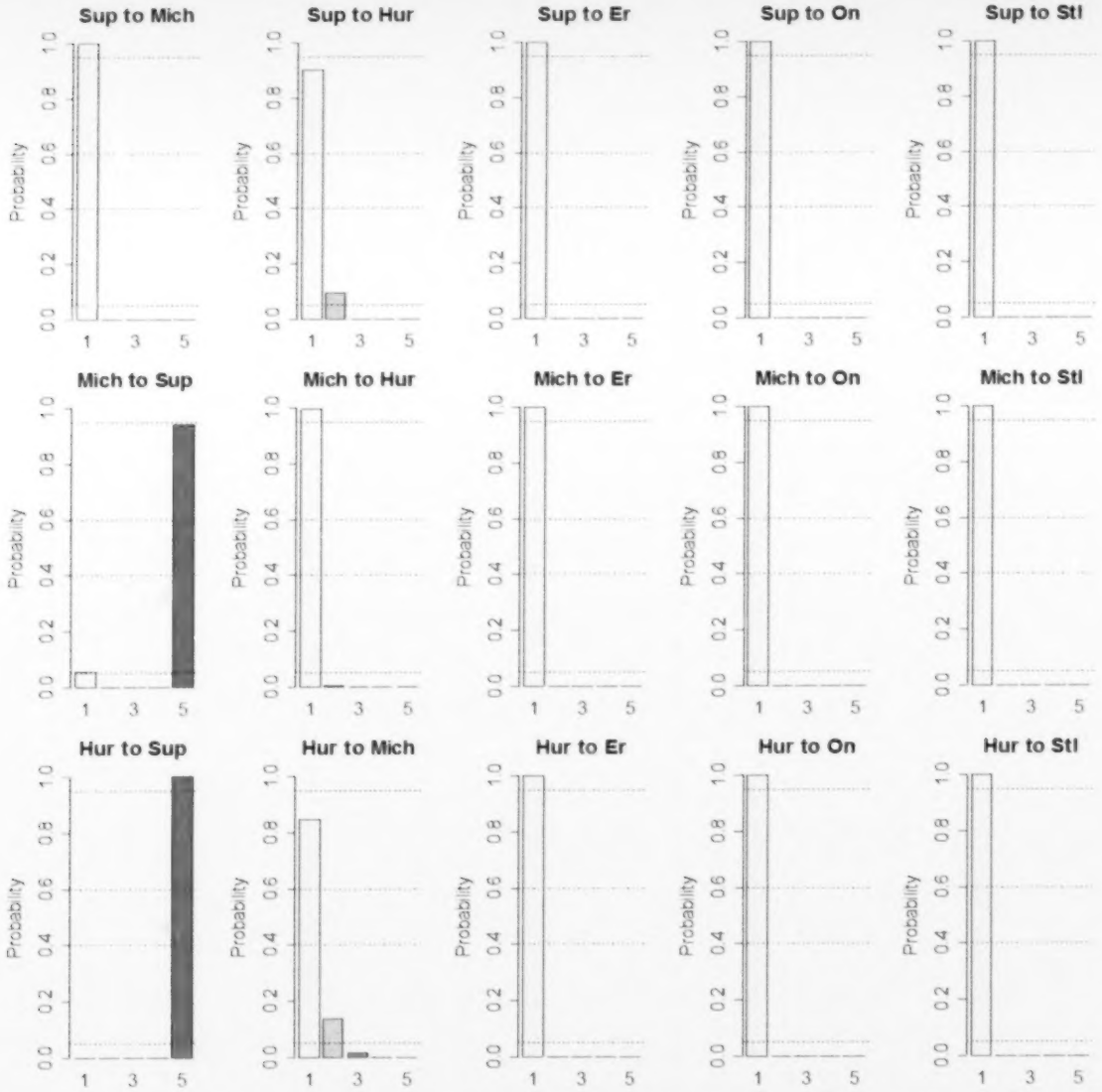
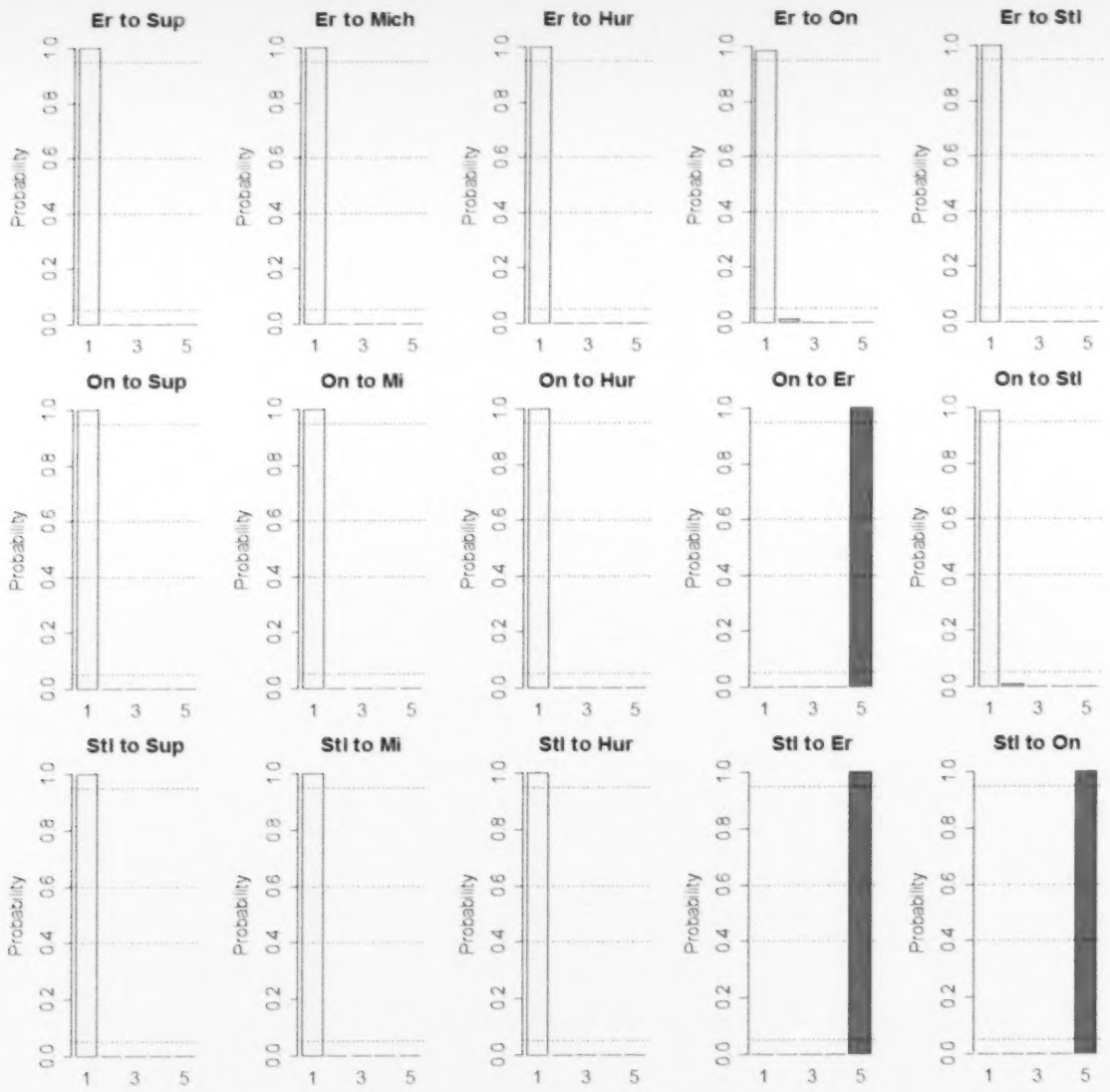


Figure 15. Ecological risk of lake to lake secondary spread of molluscs (high invasiveness) due to recreational boating activity in the GLB. ***The x-axes are consequence categories.*** *Figure panels represent the change in boater-mediated secondary spread relative to natural dispersal (see Figure 1 and Table 2 for consequence categories). Lake to lake spread is labelled at the top of each graph (e.g., upper left shows spread from an inoculation in Lake Superior to Lake Michigan). Dotted horizontal lines represent the boundaries of likelihood categories. Consequence category '5' (dark red bars) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is equal to the number of access points (and inoculation events) in each origin lake.*



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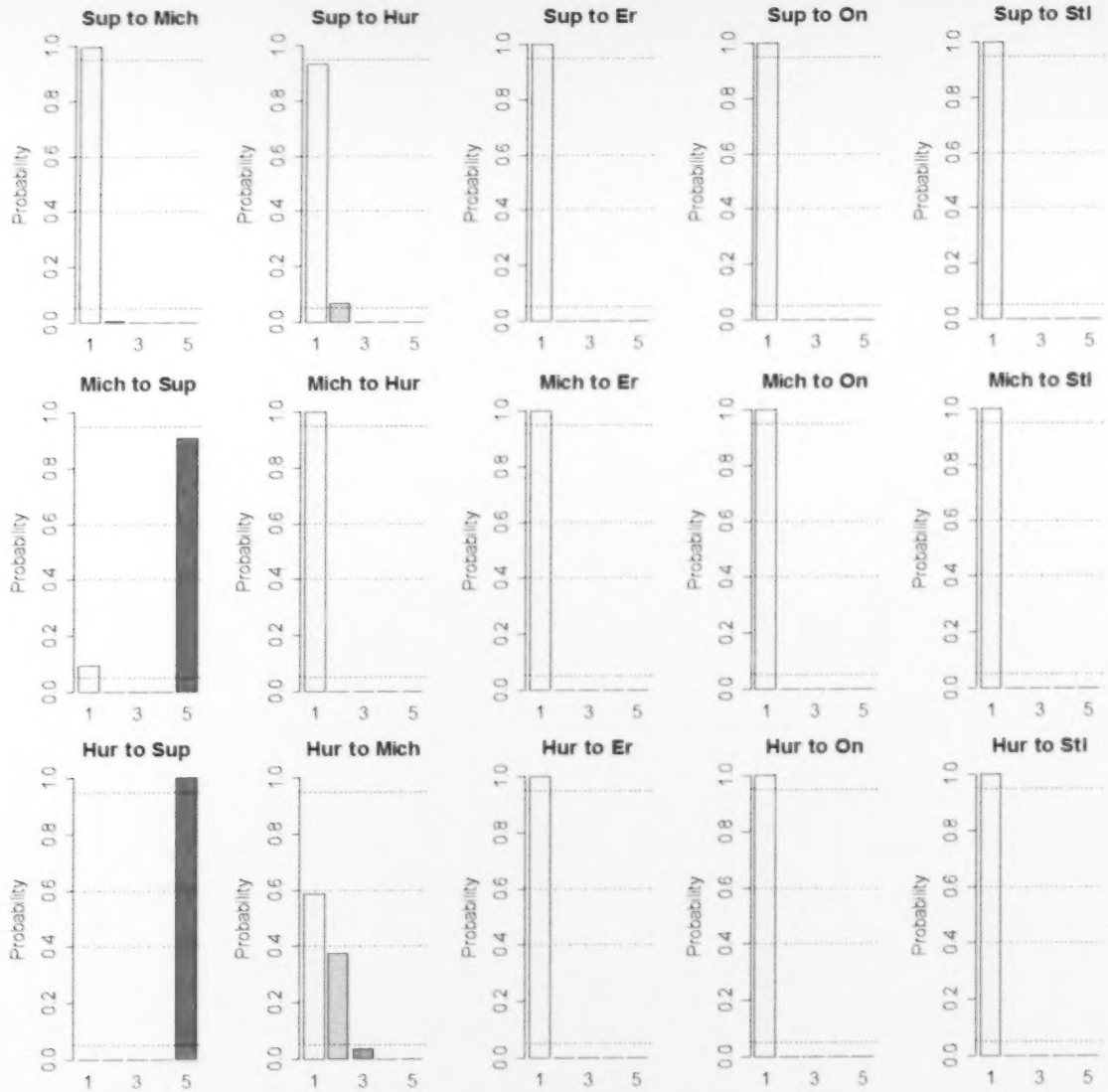
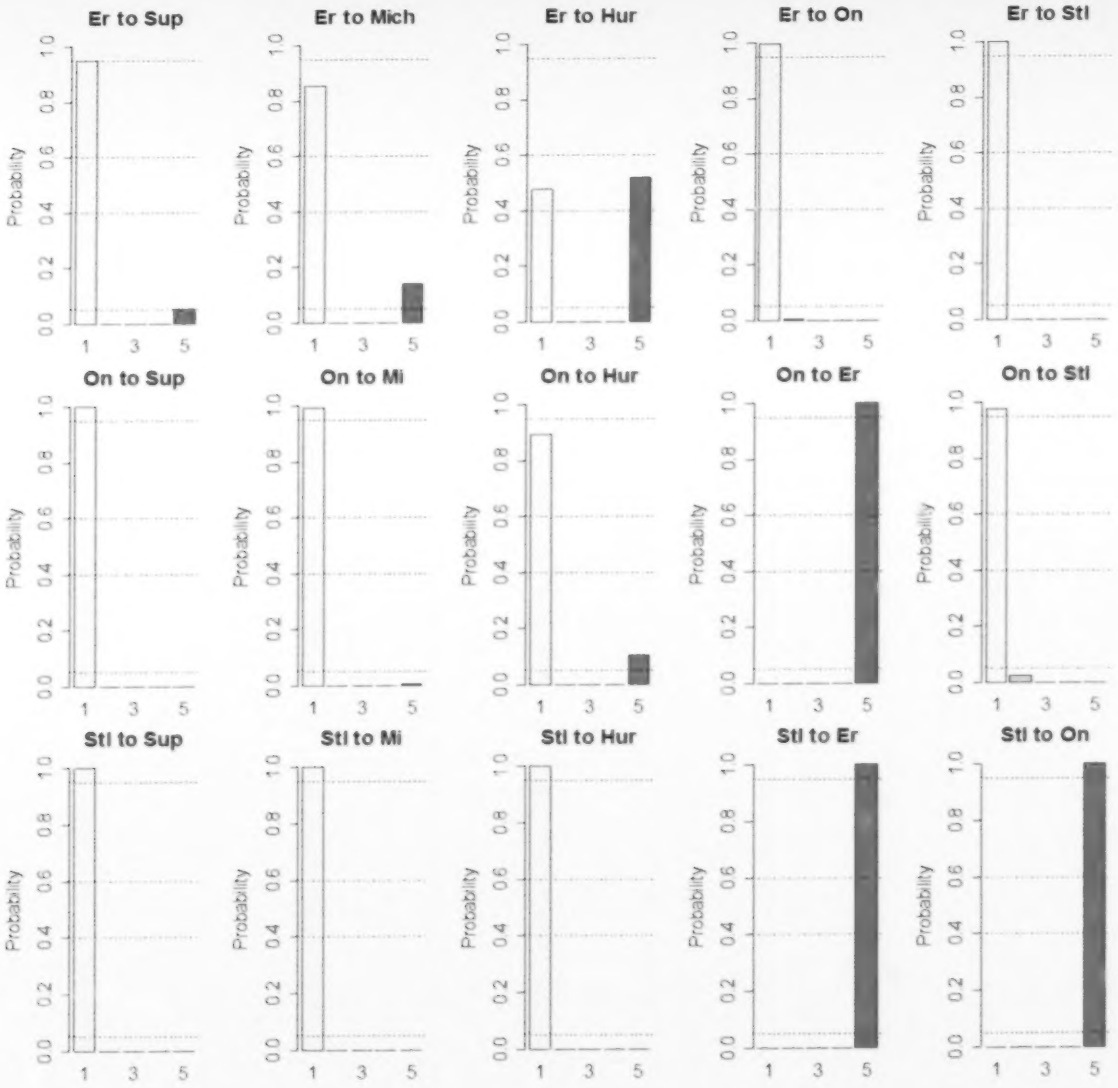


Figure 16. Ecological risk of lake to lake secondary spread of molluscs (moderate invasiveness) due to recreational boating activity in the GLB. ***The x-axes are consequence categories.*** *Figure panels represent the change in boater-mediated secondary spread relative to natural dispersal (see Figure 1 and Table 2 for consequence categories). Lake to lake spread is labelled at the top of each graph (e.g., upper left shows spread from an inoculation in Lake Superior to Lake Michigan). Dotted horizontal lines represent the boundaries of likelihood categories. Consequence category '5' (dark red bars) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is equal to the number of access points (and inoculation events) in each origin lake.*



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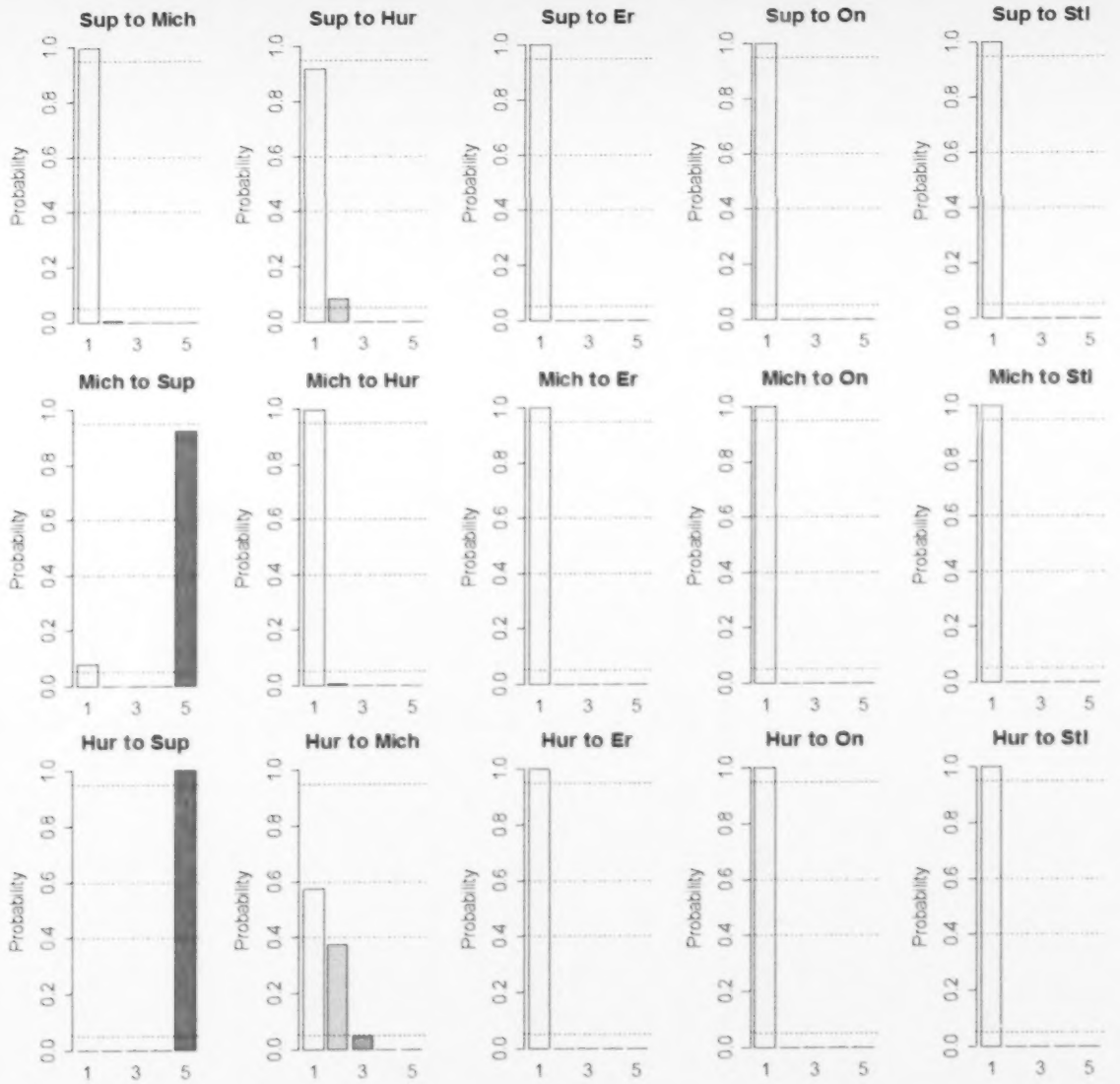
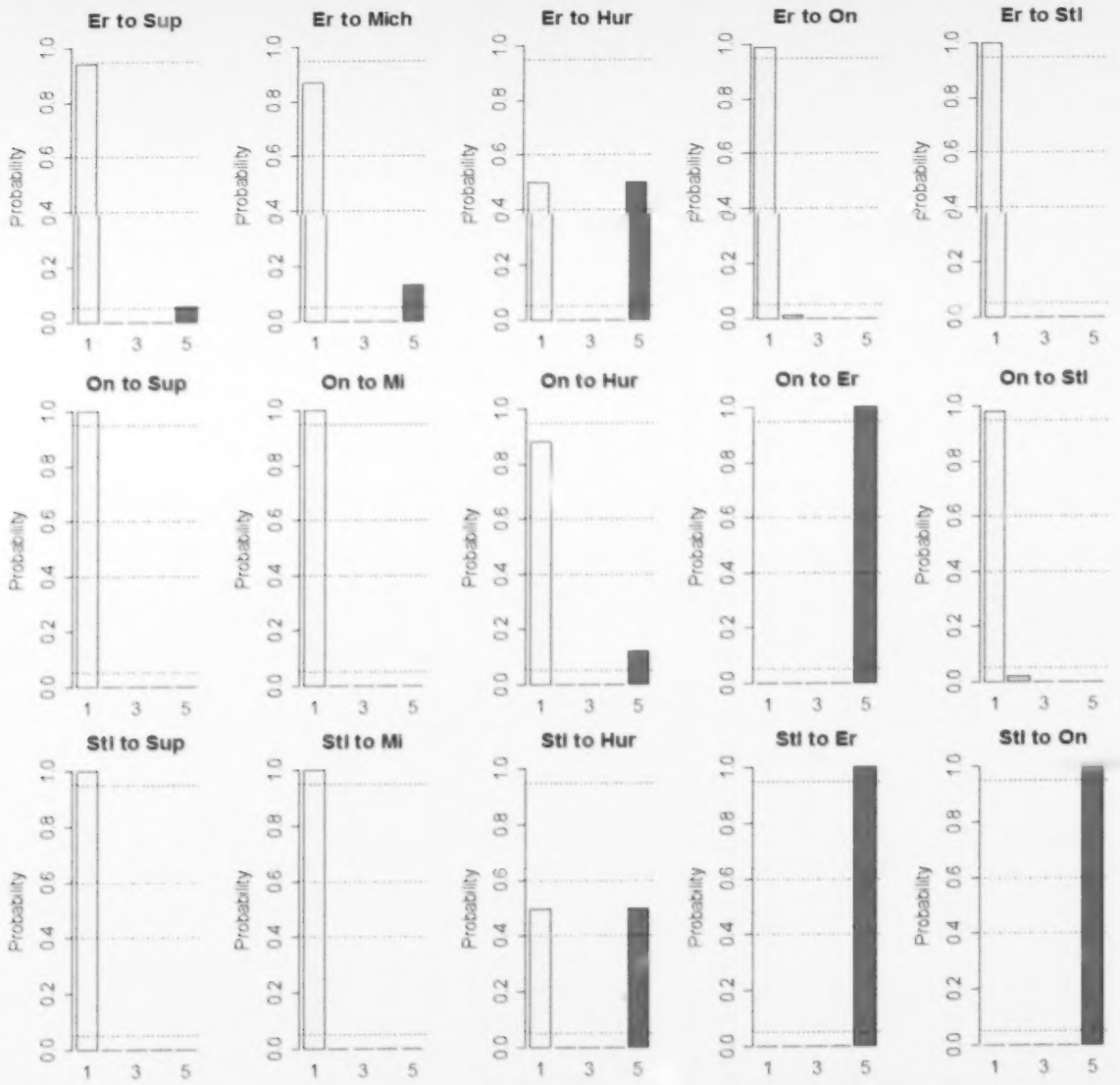


Figure 17. Ecological risk of lake to lake secondary spread of invasive macrophytes due to recreational boating activity in the GLB. ***The x-axes are consequence categories.*** *Figure panels represent the change in boater-mediated secondary spread relative to natural dispersal (see Figure 1 and Table 2 for consequence categories). Lake to lake spread is labelled at the top of each graph (e.g., upper left shows spread from an inoculation in Lake Superior to Lake Michigan). Dotted horizontal lines represent the boundaries of likelihood categories. Consequence category '5' (dark red bars) indicates that upstream boater-mediated spread has occurred within the ten-year model period. The sample size for each graph is equal to the number of access points (and inoculation events) in each origin lake.*



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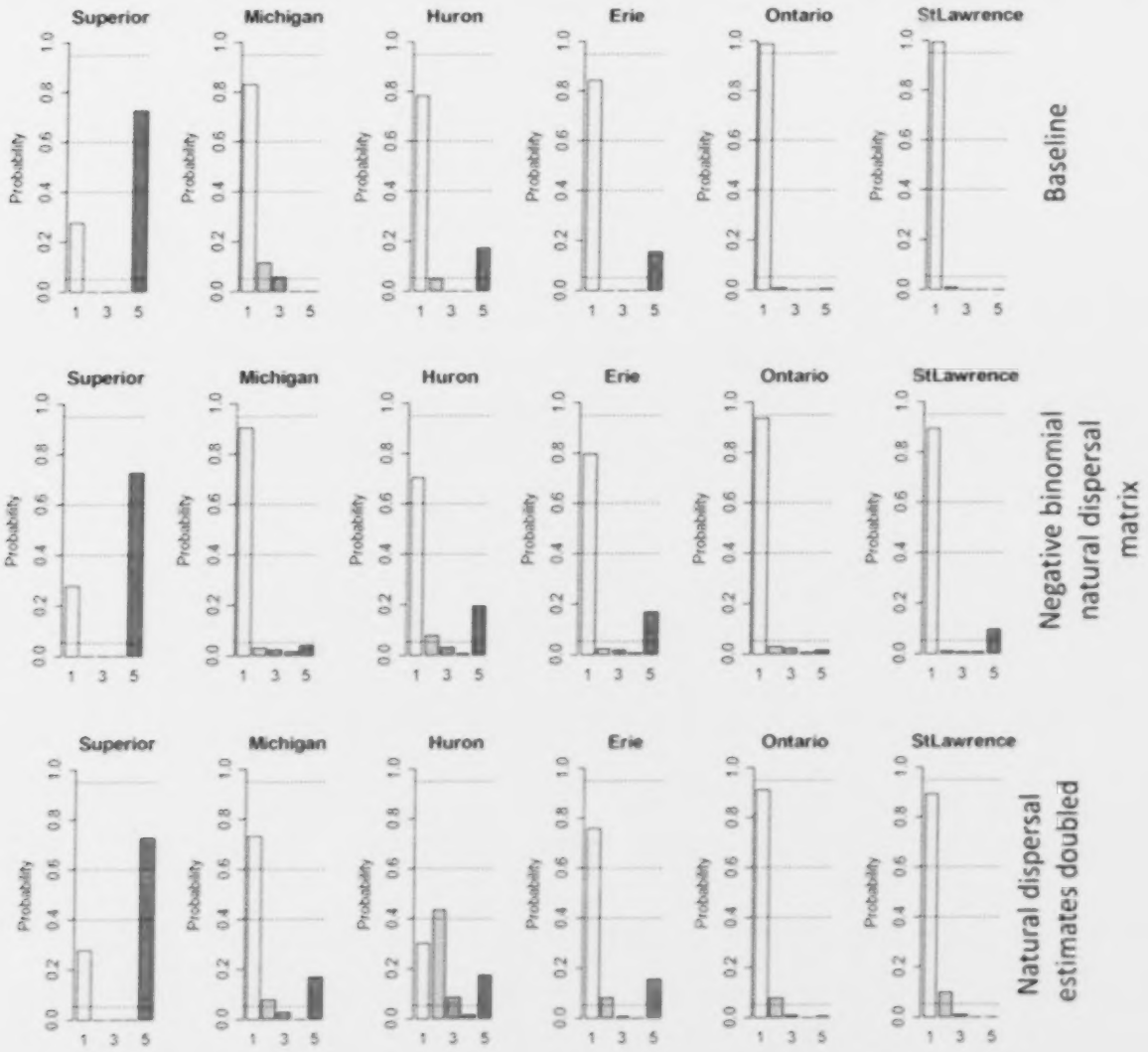

Figure 18. Results of sensitivity analysis. ***The x-axes are consequence categories.*** *Shown are baseline risk estimates for non-parthenogenetic zooplankton with high invasiveness (top row – see labels at right of panel), the risk estimate when a negative binomial natural dispersal matrix is assumed (2nd from top), the risk estimate when natural dispersal estimates are lengthened (doubled, quadrupled; 3rd and 4th from top); and, the risk estimate when model parameters (number of trips, probability of shoreline visitation, probability of release, probability of undertaking a canal trip) are reduced by 25% (5th from top).*

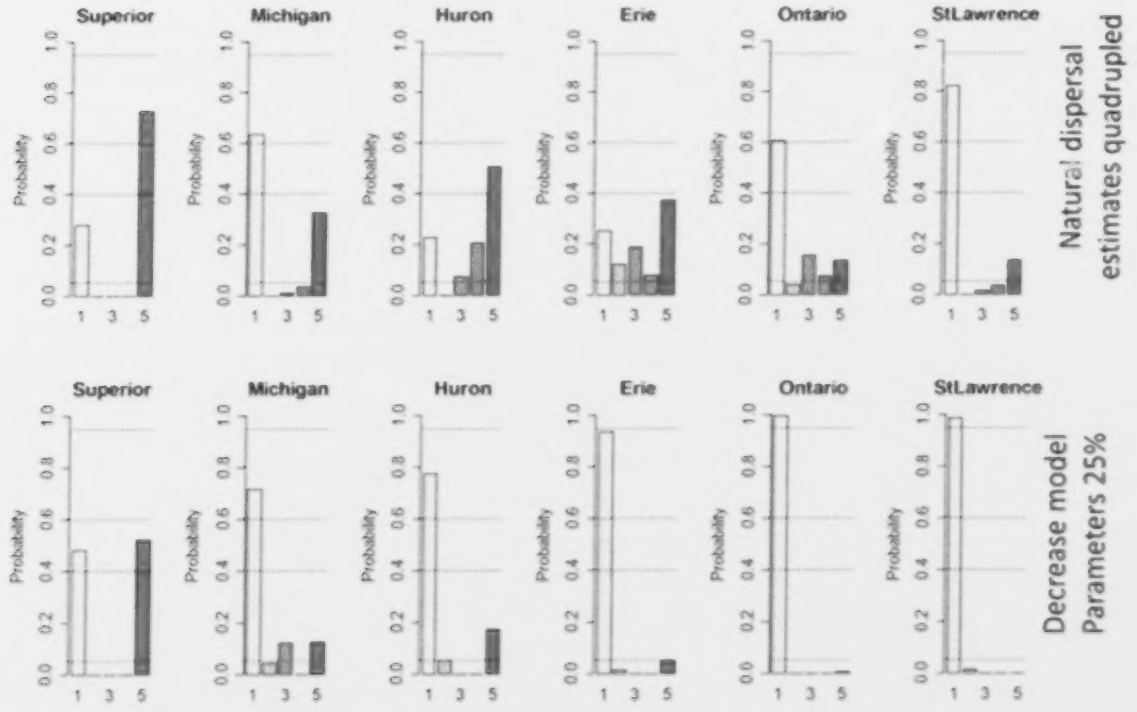

Figure 18. Continued

CONCLUSIONS AND FINAL CONSIDERATIONS

This risk assessment has identified several conclusions and considerations about the ecological risk of recreational boating for the secondary spread of aquatic invasive species in the GLB.

First, models underlying this assessment indicate that the volume of the pathway (~11 M recreational boating trips in the GLB each year) is a key factor in allowing a subset of context-dependent trips to transport AIS (plankton, molluscs, and other fouling species) when sufficient opportunity (time) exists for boater-mediated spread to occur. These findings align with other pathways of AIS introduction and spread in marine and freshwater ecosystems (e.g., baitfish activity; Drake and Mandrak 2014b, c; recreational boating in marine systems; Simard et al. 2017), where the relatively low per-boat-trip probabilities of introduction are offset by the sheer magnitude of pathway activity. The spread process was driven by interacting risky trips across lakes and years, leading to the development of satellite populations that in-turn become sources, causing an accelerating rate of spread. Therefore, results suggest that containment of newly discovered source and satellite populations, combined with measures to discourage boat fouling in those areas, are well justified as management measures to slow secondary spread.

Second, models underlying this assessment suggest that the transport of several functional groups of AIS can occur during the on-water operation of recreational boats in freshwater ecosystems. In particular, this assessment suggests that a better understanding of the role of recreational boating as a pathway of AIS can benefit by conceptualizing current and future

varieties AIS based on their functional fouling properties, such as the ability for a species to be transported as plankton, through indirect tangling, or by direct attachment on boat surfaces.

Third, there were strong correlations between species demographic rates and the resulting boater-mediated rates of spread, with highly invasive phytoplankton experiencing the most rapid spread, and moderately invasive zooplankton and molluscs experiencing the lowest rates of spread. These findings suggest that the rate of boater-mediated spread can be predicted with relatively high fidelity when the life history characteristics of newly discovered AIS are known.

Fourth, recreational boating poses a high risk of upstream spread, leading to the development of new pathways of AIS dispersal that would be unlikely to occur naturally over short (10–20 year) timeframes for many functional groups and lake-to-lake routes. For example, the boater-mediated spread of invasive phytoplankton from the St. Lawrence River, upstream through canal systems and into Lake Michigan and Lake Superior, took an average of five and nine years, respectively, a process that would not reasonably occur through natural dispersal in the same time period. While this longest upstream route was unlikely for other functional groups (e.g., zooplankton, mollusks), upstream spread between nearby lakes (e.g., Ontario to Erie, Ontario to Huron) was more common across a range of species. However, the ability of recreational boating to surpass natural downstream movement of AIS was generally poor across the GLB, though faster spread did occur by up to four years for certain functional groups. The generally low risk of downstream spread was highly sensitive to the rate of natural dispersal assumed, such that a quadrupling of natural dispersal timelines would lead to higher risk for downstream routes. Therefore, future work to better understand natural dispersal throughout large lake basins would reduce uncertainty in the ecological risk posed by recreational boating in freshwater ecosystems in Canada. The rate of spread of benthic species facilitated by the movement of anchor sediments also remains a key uncertainty, given the paucity of data describing the fouling of scud and isopoda.

An important consideration when interpreting results of this risk assessment is that model development frequently involved choosing parameters representing worst-case scenarios (e.g., the density of propagules within a boat class, the ability of water cooling systems to transport viable AIS over long distances; the release of propagules in nearshore environments). While the effect of key assumptions was tested through sensitivity analyses (Figure 18), a better understanding of model assumptions could lead to greater certainty of the risk posed by this pathway. For example, relatively small changes in the assumed values of propagule pressure or natural dispersal would have a minor effect on the results of this assessment (Figure 18), but more substantial deviations would lead to greater uncertainty, particularly for the rate of natural dispersal assumed. Also, given the high density of AIS found in engine cooling water and livewells, the ability of these niche space to transport and release viable propagules over long distances needs to be explored, including the potential for propagule retention in cooling water during boat operation. Although empirical sampling of naturally fouled boats is problematic due to the challenges of capturing rare contamination events, one approach to resolving issues around propagule pressure that would also allow for testing of hypotheses generated through this risk assessment would involve monitoring inter-lake movement of recreational boats at key choke points (e.g., St. Mary's Locks, Welland Canal).

The results of this risk assessment may be broadly applicable to a variety of Canada's large lake ecosystems, such as Lake Winnipeg and Lake Winnipegosis, Great Bear and Great Slave Lake, Lake Athabasca, and many others that are spatially and ecologically similar to the GLB. While the timelines of spread will vary across Canada's large lake ecosystems (with consequences depending on background rates of natural dispersal), results of this assessment indicate that the boater-mediated spread of AIS can substantially circumvent the background

rate of natural dispersal, suggesting that increased attention to recreational boating as a pathway of secondary spread within large lake ecosystems is warranted.

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APPENDIX 1.0 QUESTIONNAIRE TO DOCUMENT RECREATIONAL BOATING IN THE GLB

This was distributed to Ontario boaters as part of the Ontario Invading Species Survey (Ontario Ministry of Natural Resources and Forestry).

This survey contains 31 questions divided into 5 sections - Section 1: Boating Habits; Section 2: Recreational Fishing Habits; Section 3: Source of Information; Section 4: Social Impacts of Invasive Species; and Section 5: About You

Section 1 – Boating Habits

1. Please enter the 6 digit postal code of your primary residence _____

2. Did you own and use a power driven vessel or sailboat in 2009?

Yes ☐ No ☐ → If no: please go to **Question 14**

3. Please indicate the type of boat owned in 2009. If you owned and used more than one boat, please respond for the boat that was used most frequently in 2009.

Boat Type	Size of boat? (length in feet)	Horsepower of boat? (if applicable)	Hull type (e.g., wood, aluminium, fibreglass, etc.)
1. Power-driven vessel (e.g., fishing boat, day cruiser)			
2. Boat with ballast (e.g., wakeboard boat)			
3. Sailboat			
4. Personal watercraft (e.g., Jetski)			
5. Other (Specify):			

Please answer Questions 4 to 13 according to the boat that is listed in Question 3.

3. What were the main reasons for using this boat in 2009?
(Please check yes for **each** use.)

Boat use	Yes
Fishing	☐
Water sports (e.g. skiing, jet ski...)	☐
Sailing	☐
Cruising or sightseeing	☐

Boat use	Yes
Hunting	☐
Camping	☐
Other (please specify):	☐

4. **Where was this boat stored/kept during the 2009 boating season? If this boat was stored/kept at more than one location, please identify the location where this boat was stored most frequently during the boating season:**

☐ On land at my primary residence

☐ In the water at my primary residence

☐ On land at a location other than my primary residence (e.g. cottage, camp, trailer park)

☐ In the water at a location other than my primary residence (e.g. cottage, camp, trailer park)

☐ On land at a marina facility or boat club.

☐ In the water at a marina facility or boat club.

☐ Other: _____

Please list the nearest town/city and province where your boat was stored/kept most frequently during the 2009 boating season:

City/Town: Province:

5. **In 2009, did you use this boat on the Great Lakes or connecting waterways?**

(Includes Lake Superior, Lake Michigan, Lake Huron, Lake St. Clair, Lake Erie, Lake Ontario, St. Mary's River, St. Clair River, Detroit River, Niagara River and St. Lawrence River).

☐ Yes

☐ No (Proceed to Question 7)

If yes, please describe trips taken by boat on the Great Lakes or connecting waterways in 2009. If you took more than ten *different* trips (i.e., trips to different locations), please describe only the ten most-frequent boating trips below.

Great Lakes' Location	Departure Point	estination and stop-over port(s) visited?	Approximate round-trip boating distance (km)?	Approximate number of times trip was taken in 2009?
e.g. Lake Ontario	Bronte Harbour Oakville, ON	N/A, only boated locally	10 km	4
e.g. Lake St. Clair	Windsor Yacht Club Windsor, ON	Lands' End Marina, Harrison, MI	60 km	2

6. **In 2009, did you use this boat on any inland lakes or rivers in Ontario (i.e., Ontario locations other than the Great Lakes or connecting waterways)?**

☐ Yes

☐ No (Proceed to Question 8)

If yes, please list the name(s) of EACH lake/river, including the name of the closest town and the number of trips taken in 2009. If you used this boat at more than ten locations, please list only the ten most-frequent locations below.

Lake/River visited	Closest town to launch site	Approximate number of trips
e.g., Lake Simcoe	Beaverton	10

7. In 2009, did you use this boat outside of Ontario and the Great Lakes

☐ Yes

☐ No (Proceed to Question 9)

If yes, please list EACH location visited, the closest town/city to the launch site, and the number of trips taken in 2009. If more than three, please list only the three most-frequent locations below.

Lake/River/Ocean visited	Closest town to launch site (include province/state)	Approximate number of trips
e.g. Lake Winnipeg	Winnipeg Beach, Manitoba	1

8. How often did you do each of the following?

(Please check **one** response for **each** step.)

Steps Taken:	Always	Sometimes	Never	Does Not Apply
Conduct visual inspection of boat and trailer and remove attached plants and animals	☐	☐	☐	☐
Drain water from boat, including bilge and live well	☐	☐	☐	☐
Allow boat to dry for 5 days	☐	☐	☐	☐
Rinse boat with high pressure water	☐	☐	☐	☐
Rinse boat with hot water	☐	☐	☐	☐
Clean plants and animals from anchor and full length of anchor line	☐	☐	☐	☐
Clean plants and animals from downrigger cables, and fishing line	☐	☐	☐	☐
Flush motor's intake port with hot water	☐	☐	☐	☐
Other (please specify):	☐	☐	☐	☐

9. **If you did not always clean this boat and equipment as indicated in Question 9, please indicate why.** (Check all that apply)

☐ Didn't see this as being important

☐ Didn't have the equipment needed

☐ It took too long

☐ Did not know how to do it

☐ Does not apply, I always cleaned my boat and equipment after removal from a lake or river

☐ Does not apply, I only boat on one waterbody

☐ Other _____

10. **If you did not always clean this boat and equipment as indicated in Question 9, what would encourage you to do so?** (Check all that apply)

☐ Information on the benefits of cleaning

☐ Information on how to do it

☐ Assurance that others are doing it too

☐ Equipment at boat launches and marinas to assist in cleaning

☐ Does not apply, I always clean my boat and equipment after removal from a lake or river

☐ Does not apply, I only boat on one waterbody

☐ Other _____

11. **If you had the proper information, and convenient access to the necessary equipment, would you clean your boat before launching into another body of water?**

☐ Yes

☐ No

☐ Maybe

☐ Don't Know

☐ Does not apply, I only boat on one waterbody

☐ Does not apply, I always clean my boat and equipment

12. How would you prefer to receive information on proper boat and equipment cleaning techniques?

- ☐ Television advertising
- ☐ Print advertising (newspaper/magazine)
- ☐ Radio advertising
- ☐ Brochures
- ☐ Website
- ☐ Signs and information at boat launches and marinas
- ☐ Highway billboards
- ☐ Hands-on demonstration at boat launches and marinas
- ☐ Information in the Ontario Fishing Summary
- ☐ Direct mail or Email
- ☐ Other _____
- ☐ Do not need information as I only boat on one waterbody
- ☐ Do not need information as I always clean my boat

Section 2 – Recreational Fishing Habits

13. Did you fish in 2009?

Yes ☐ No ☐ → If no: please go to **Question 20.**

14. How often did you use the following bait? (Please check **one** response for **each** type of bait.)

Types of Bait/Tackle	Always	Sometimes	Never
Live Baitfish	☐	☐	☐
Dead baitfish	☐	☐	☐
Fishparts/roe	☐	☐	☐
Artificial Lures	☐	☐	☐
Crayfish	☐	☐	☐
Worms	☐	☐	☐
Leeches	☐	☐	☐
Frogs	☐	☐	☐
Other (please specify):	☐	☐	☐

15. If you used live bait (fish, worms, leeches, crayfish, frogs); how did you obtain it?

(Please check **one** response for **each** method.)

I obtained live bait by...	**Always**	**Sometimes**	**Never**
Buying it	☐	☐	☐
Collecting it from the same water body or location I was fishing in	☐	☐	☐
Collecting it from a different water body or location than the one I was fishing in	☐	☐	☐
Using someone else's leftover bait	☐	☐	☐
Other (please specify):	☐	☐	☐
Did not use live bait	☐		

16. What did you do with your leftover bait at the end of the day?

(Please check **one** response for **each** action.)

Any leftover crayfish, fish, frogs, leeches, and fish parts/roe are...	**Always**	**Sometimes**	**Never**
Released into the lake or river	☐	☐	☐
Returned to the bait shop	☐	☐	☐
Given away to other anglers	☐	☐	☐
Disposed of on land or in garbage	☐	☐	☐
Frozen or salted for later use	☐	☐	☐
Never have left over bait	☐		
Other (please specify):	☐	☐	☐

Any leftover worms were ...	**Always**	**Sometimes**	**Never**
Released into the lake or river	☐	☐	☐
Given away to other anglers	☐	☐	☐
Disposed of on land	☐	☐	☐
Disposed of in garbage	☐	☐	☐

Any leftover worms were ...	Always	Sometimes	Never
Never have left over worms	☐		
Other (please specify):	☐	☐	☐

17. If you always or sometimes released unused bait into a body of water, please indicate why? (Check all that apply)

- ☐ Did not want to unnecessarily kill the bait
- ☐ Water is a convenient place for disposal
- ☐ Did not want to transport unused bait after fishing is done
- ☐ Will smell or attract wildlife if dumped on ground or in garbage
- ☐ No place (or facility) at boat launch or marina for disposing of unused bait
- ☐ Other _____
- ☐ Does not apply as I never released unused bait into a body of water.

18. How would you prefer to receive information on proper disposal of unused bait?

- ☐ Television advertising
- ☐ Print advertising (newspaper/magazine)
- ☐ Radio advertising
- ☐ Brochures
- ☐ Website
- ☐ Signs and information at boat launches and marinas
- ☐ Highway billboards
- ☐ Information in the Recreational Fishing Regulations Summary
- ☐ Direct mail or email
- ☐ Reminder when buying bait
- ☐ Reminder when buying fishing license
- ☐ Other _____
- ☐ Do not need information as I use artificial lures

Section 3 – Source of Information

19. Have you heard or read about invading species?
(Also known as invasive, exotic, non-native, non-indigenous or alien species)

Yes ☐ No ☐ → If no: please go to **Question 28.**

20. Select the organizations or agencies from which you have received information about invading species? (Please check yes or no for each agency.)

Organizations and Agencies	Yes	No
Ontario Ministry of Natural Resources	☐	☐
Department of Fisheries and Oceans	☐	☐
Canadian Coast Guard	☐	☐
Environment Canada	☐	☐
Ontario Federation of Anglers and Hunters	☐	☐
A cottager's or lake association	☐	☐
Fishing/Boating Club	☐	O
School	☐	O
I have not received any information about invading species	☐	☐
I am not sure which organization/agency provided the information		
Other (please specify):	☐	☐

21. Select all the sources from which you have heard of or read about invading species.

(Please check yes or no for each source.)

Source	Yes	No
Internet	☐	☐
Newspaper or magazine articles	☐	☐
Television	☐	☐
Radio	☐	☐
Brochures or fact sheets	☐	☐
Billboards	☐	☐
Family/Friends	☐	☐
Recreational fishing regulations summary	☐	☐
Postings of information at a marina or bait/tackle shop	☐	☐

Source	Yes	No
Bait bucket stickers, fish rulers, and bumper stickers	☐	☐
Signs provided at a boat launch	☐	☐
Invading Species Hotline (1-800-563-7711)	☐	☐
Display at sport or trade shows	☐	☐
Other (please specify):	☐	☐

22. Based on your selection(s) above, what source provided you with the best information on how to avoid spreading invading species from one water body to another?

(Please write down **only one** source.)

The best source of information was:

23. In your opinion, is it important that anglers and boaters take precautions to prevent the spread of invading species from one water body to another?

Yes ☐ No ☐ → If no: please go to **Question 26.**

24. How important is it to take precautions to prevent the spread of each of the following invading species? (Please check **one** response for **each** species.)

Taking precautions to prevent the spread of invading species is….

Invading Species	Very Important	Somewhat Important	Not Very Important	Not Important	Don't Know
Zebra mussels	☐	☐	☐	☐	☐
Spiny and Fishhook water fleas	☐	☐	☐	☐	☐
Rusty crayfish	☐	☐	☐	☐	☐
Round Goby	☐	☐	☐	☐	☐
Eurasian Ruffe	☐	☐	☐	☐	☐
Asian Carp	☐	☐	☐	☐	☐
Purple loosestrife	☐	☐	☐	☐	☐
Eurasian water milfoil	☐	☐	☐	☐	☐
Rainbow Smelt	☐	☐	☐	☐	☐
Other	☐	☐	☐	☐	☐

Section 4 – Social Impacts of Invasive Species

25. Has the presence of invading species affected any of your recreational or business activities or the value of your property? (Please check **one** response for **each** activity/value.)

Activity/Value	Negatively Affected	Positively Affected	Not Affected	Does Not Apply
Swimming	☐	☐	☐	☐
Boating	☐	☐	☐	☐
Fishing	☐	☐	☐	☐
Hunting and Trapping	☐	☐	☐	☐
Enjoyment of the natural environment	☐	☐	☐	☐
Business revenue	☐	☐	☐	☐
Property value	☐	☐	☐	☐
Other (please specify):	☐	☐	☐	☐

26. Have you changed your recreational habits to avoid invading species?

Yes ☐ No ☐

If yes: What changes have you already made?

(Please check yes or no for each change.)

I have made changes to ...	Yes	No
Location	☐	☐
Timing of activity	☐	☐
Type of gear used	☐	☐
Other (please specify):	☐	☐

Section 5 – About You

27. In what year were you born?

28. Are you male ☐ or female ☐?

29. What is the highest level of education you have completed?

(Please check only one response.)

No formal education	☐
Elementary	☐
High school	☐
Vocational/Trade school	☐
University/College	☐
Post Graduate (e.g. MBA, PhD...)	☐
Other (please specify):	☐

30. Please use the space below for any comments or suggestions you would like to include about the spread of invading species in Ontario's waters and related programs.

Thank you for your time and cooperation.
We invite you to call the Invading Species Hotline at 1-800-563-7711
to get more information or report an invading species sighting.

The information on this questionnaire is collected under the authority of the Fish and Wildlife Conservation Act, R.S.O. 1999, for fisheries management purposes. Under the Freedom of Information and Protection of Privacy Act (1987), personal information will remain confidential unless prior consent is obtained.

APPENDIX 2.0 MODEL PARAMETERS AND DEMOGRAPHIC CHARACTERISTICS

Table A2-1. Model Parameters and demographic characteristic used to estimate secondary spread due to recreational boating.

Parameter	Description	*Values*
α	Shape coefficient of the risk-release relationship. Also known as the natural logarithm of the per-propagule probability of establishing (see Leung et al. 2004 and National Research Council 2011 for risk-release relationships)	Phytoplankton: $\alpha = 0.9$ Zooplankton: $\alpha = 0.1, 0.05, 0.001$ Molluscs: $\alpha = 0.1, 0.05$ Macrophytes: $\alpha = 0.9$
c	The existence and magnitude of an Allee effect within the probability of establishment equation from Leung et al. (2004) and National Research Council (2011)	$c = 1$ (absence of Allee effect)
N_H	Initial population size (propagules/m^3 or propagules/m^2) following dispersion into surrounding environment	Varies based on estimated propagule pressure for an individual event, which is a function of boat type (power, sail, or manual) and storage type (in-water vs day-launch). Also modified by dispersion following release into the environment (*Disp*)
X_0	X_0 is time (years) at which an introduced population reaches 50% of maximum population density.	Fixed within functional groups. Phytoplankton: $X_0 = 0.5$ Zooplankton: $X_0 = 1, 2, 5$ Molluscs: $X_0 = 2, 4$ Macrophytes: $X_0 = 5$
k	Steepness of logistic curve describing population growth.	$k = 1$
Disp	The physical dispersion of propagules (i.e., change in population density) following release into the environment	Uniform distribution (0,1)
T	Absolute number of yearly recreational boater trips within the Great Lakes (U.S. and Canadian trips combined)	11.8 million
PIntl	Estimated per-trip probability that a trip will cross an international boundary	P = 0.00039
PLocks	Estimated per-trip probability that a trip will transit through connecting channels with locks (e.g., St. Marys River, Welland Canal)	St. Marys River, P = 0.00039 Welland Canal System, P = 0.00039
M	Number of yearly trips leaving an individual recreational access site out of 1717 total GLB ports (487 CAN, 1230 U.S.)	Neg. binom. (k = 1, μ = 6,517 (U.S.), = 7,806 (CAN))

APPENDIX 3.0 TIMELINES OF SECONDARY SPREAD DUE TO RECREATIONAL BOATING

PHYTOPLANKTON FUNCTIONAL GROUP

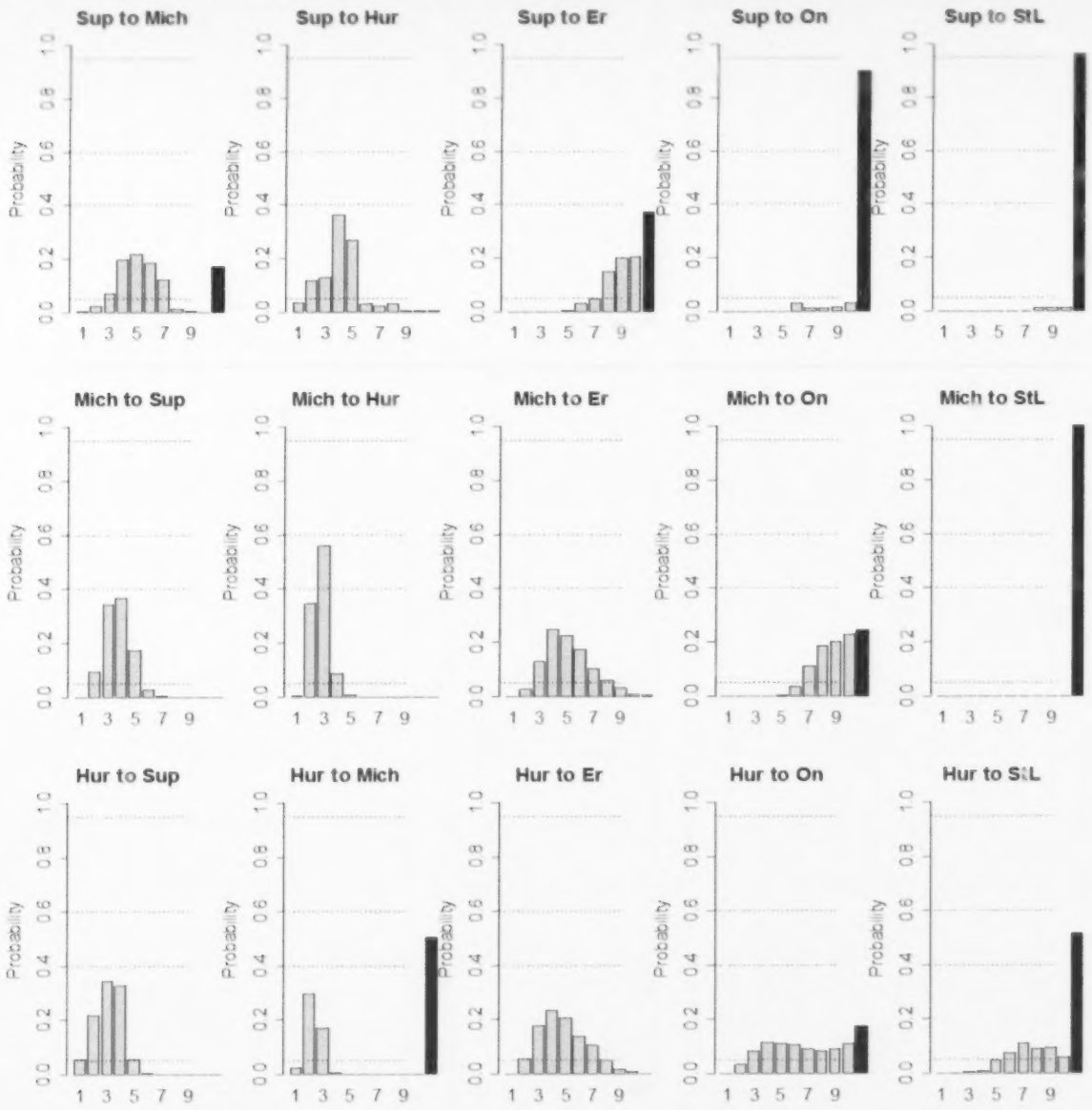

Figure A3-1. Timelines of secondary spread due to recreational boating for the phytoplankton functional group. ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

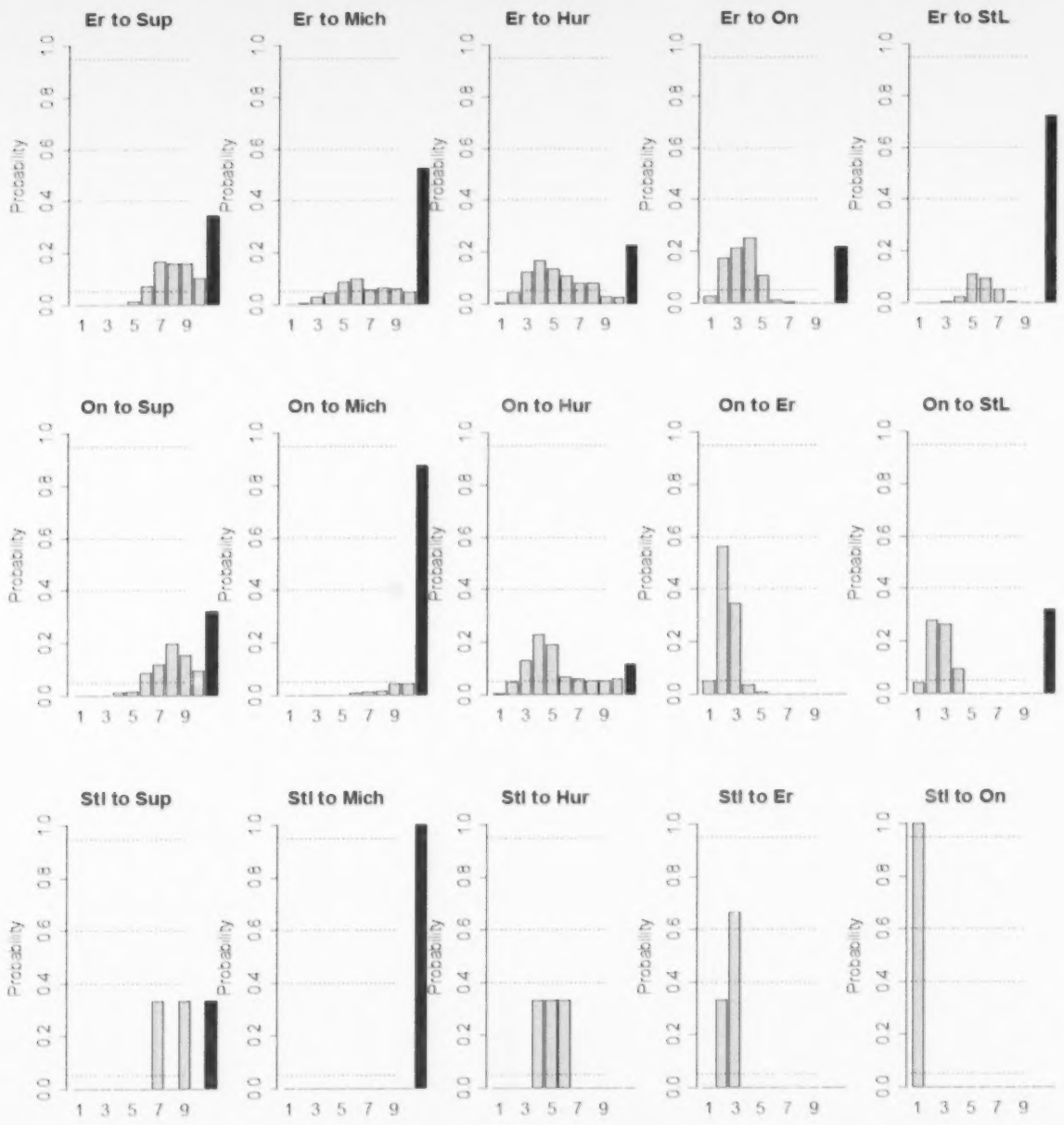

Figure A3-1. Continued.

PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP

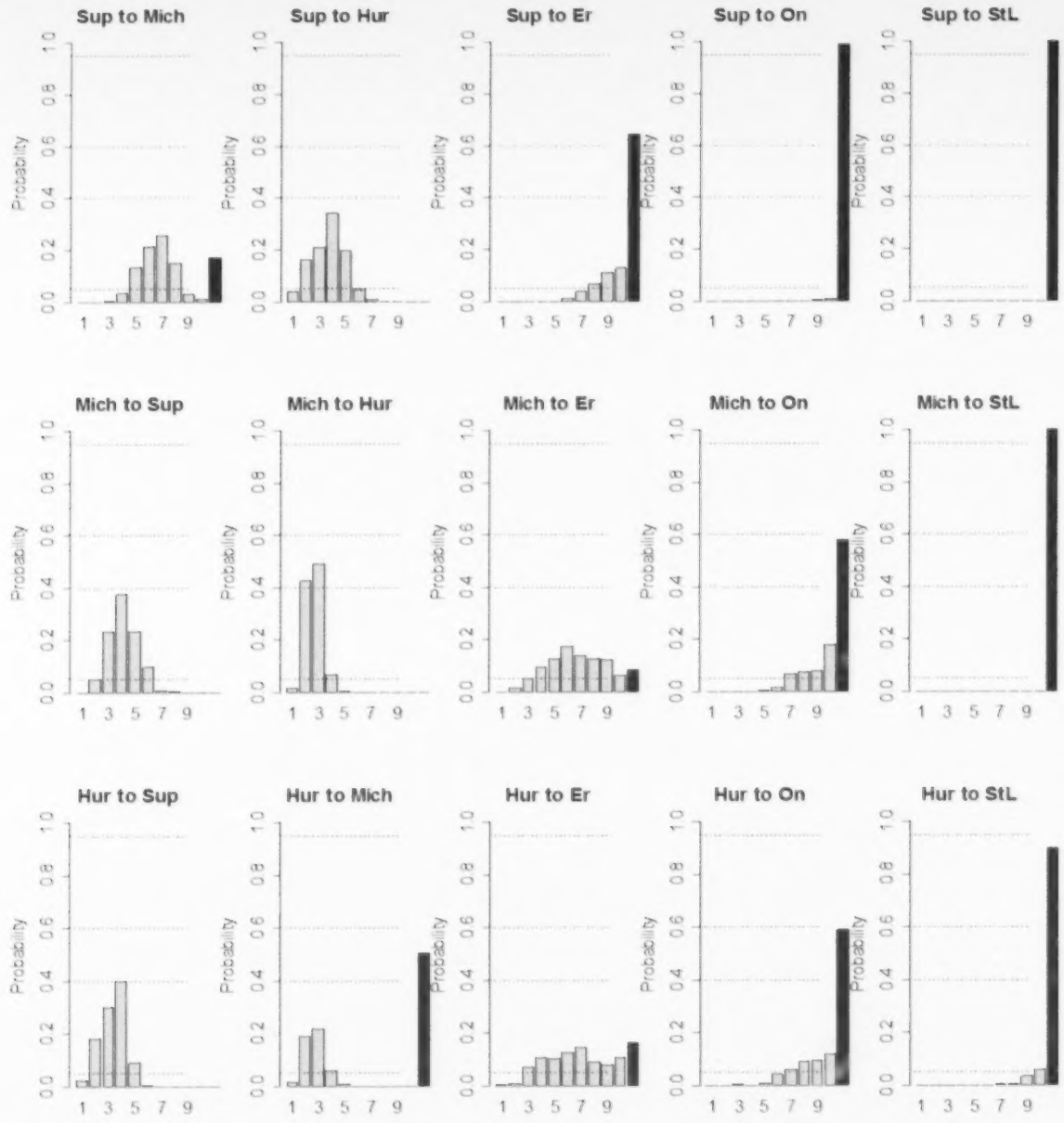

Figure A3-2. Timelines of secondary spread due to recreational boating for the parthenogenetic zooplankton functional group. ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

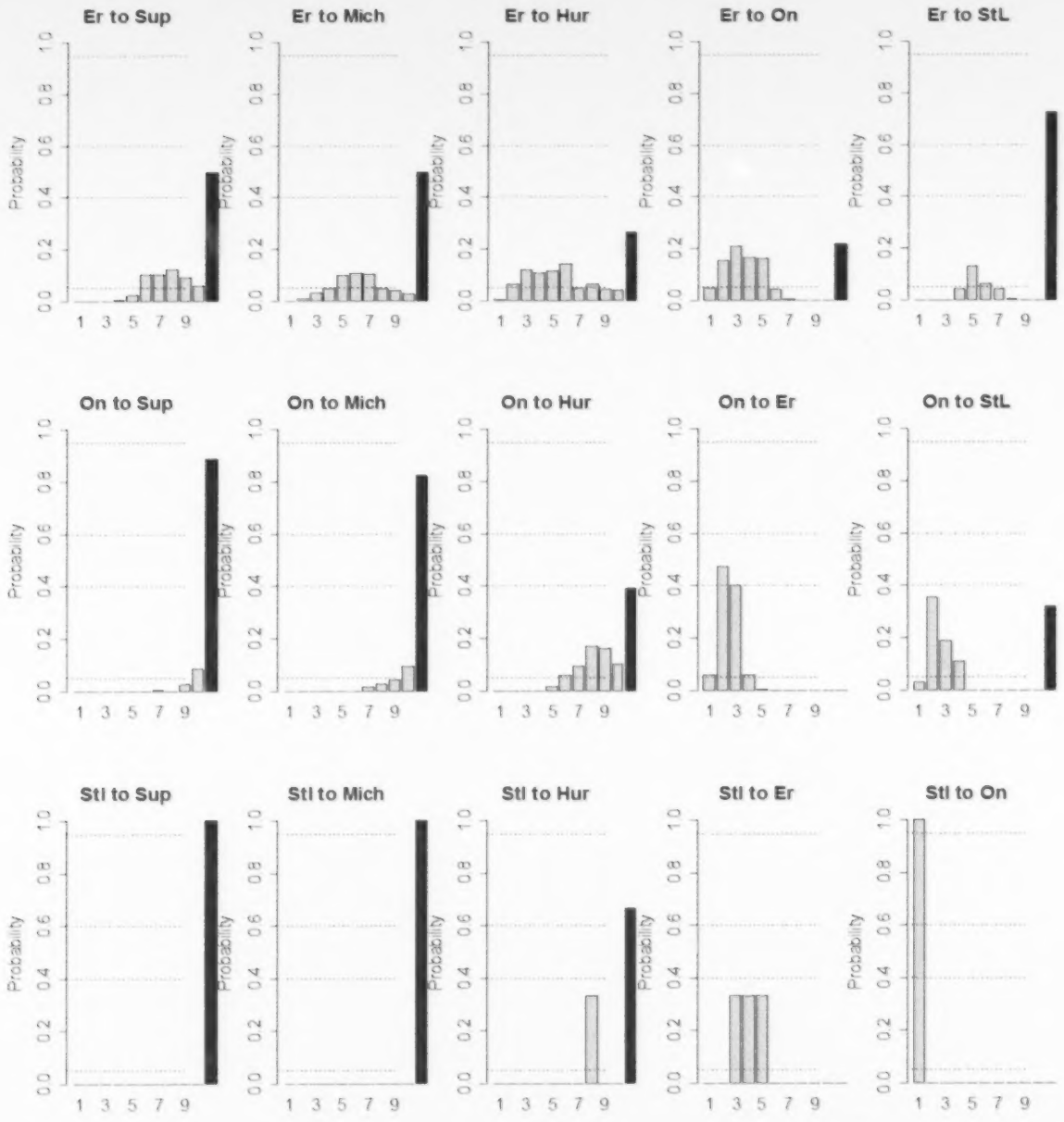

Figure A3-2. Continued.

NON-PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP (HIGH INVASIVENESS)

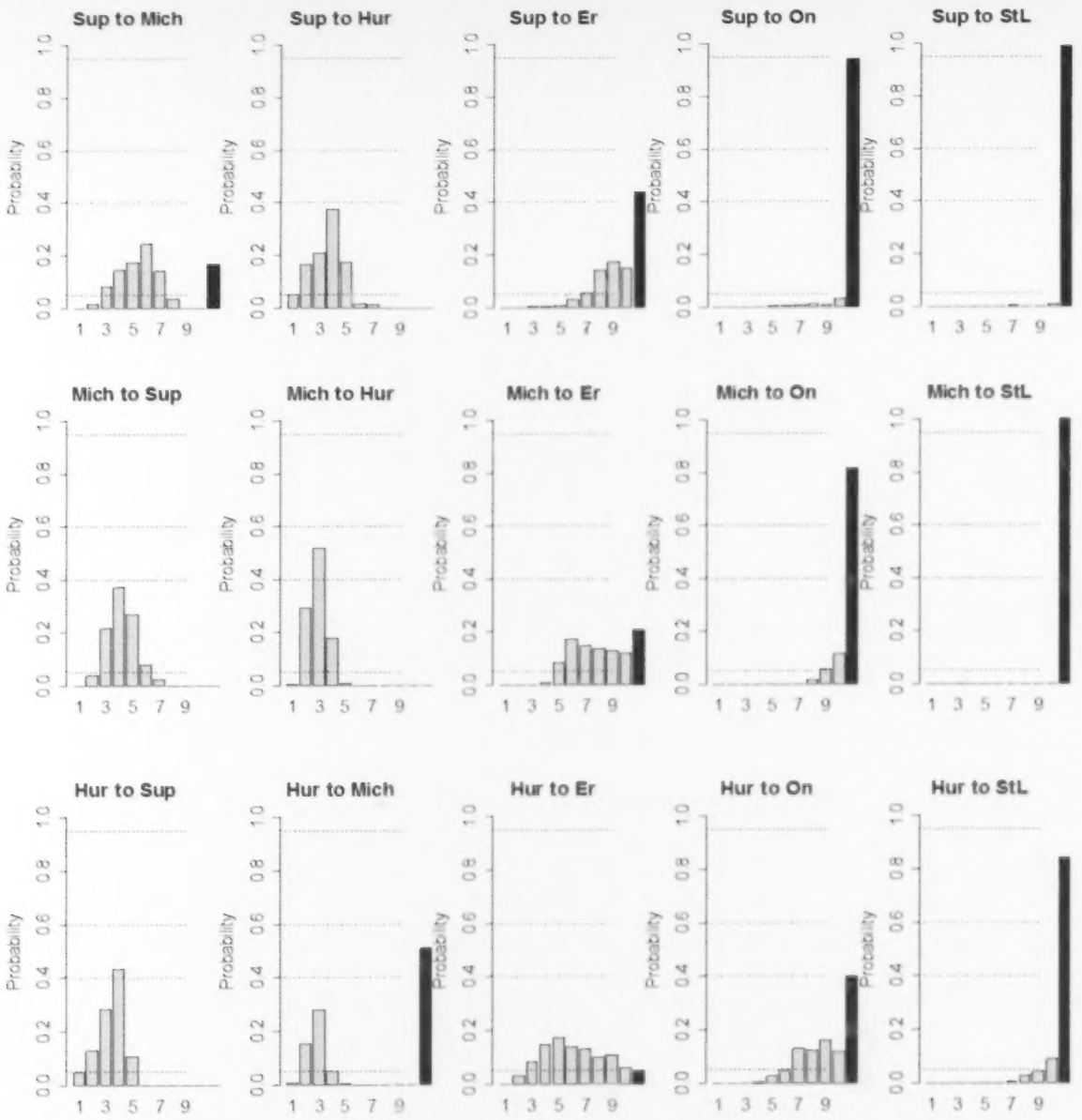

Figure A3-3. Timelines of secondary spread due to recreational boating for the non-parthenogenetic zooplankton functional group (high invasiveness). ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

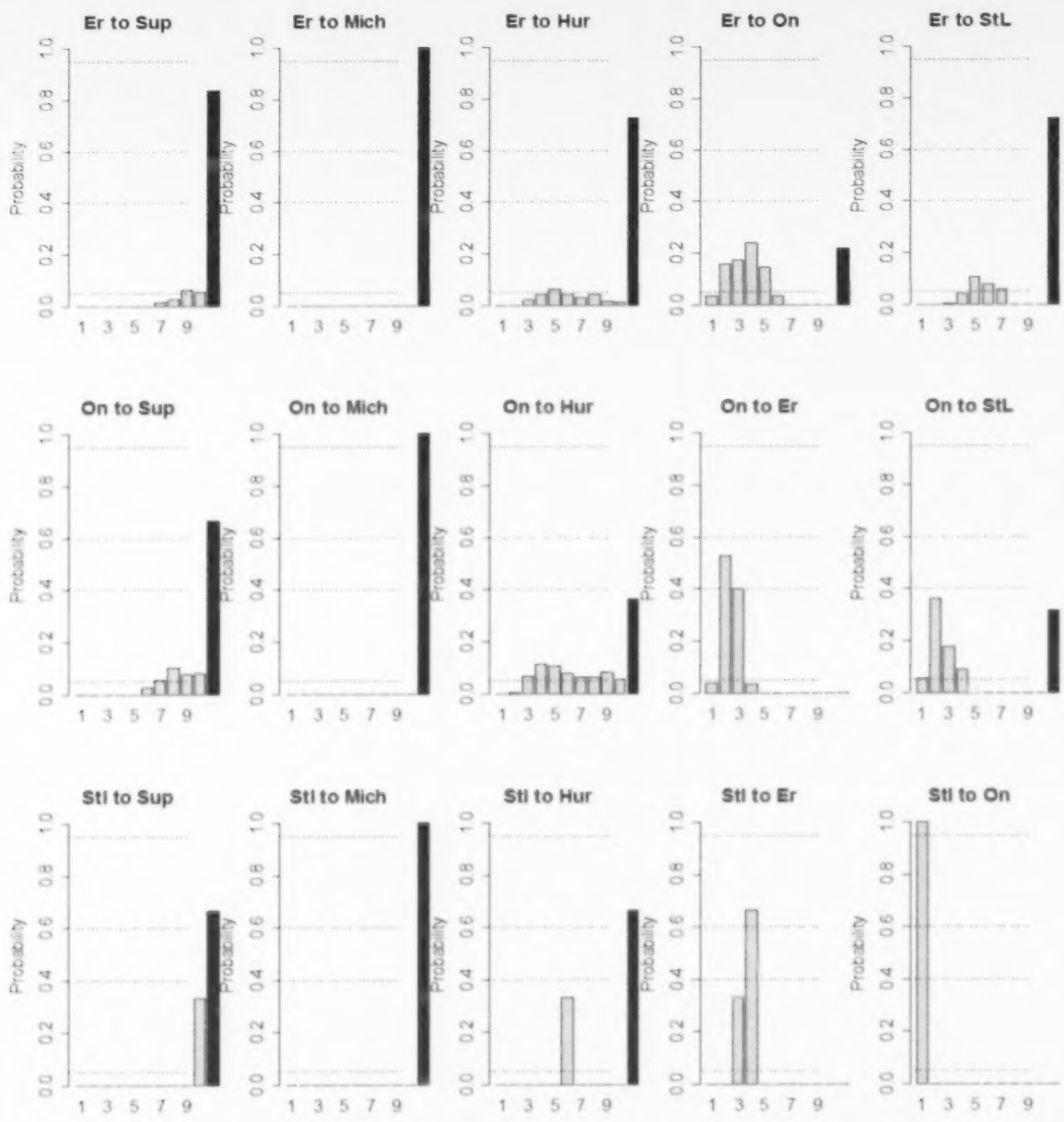

Figure A3-3. Continued.

NON-PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP (MODERATE INVASIVENESS)

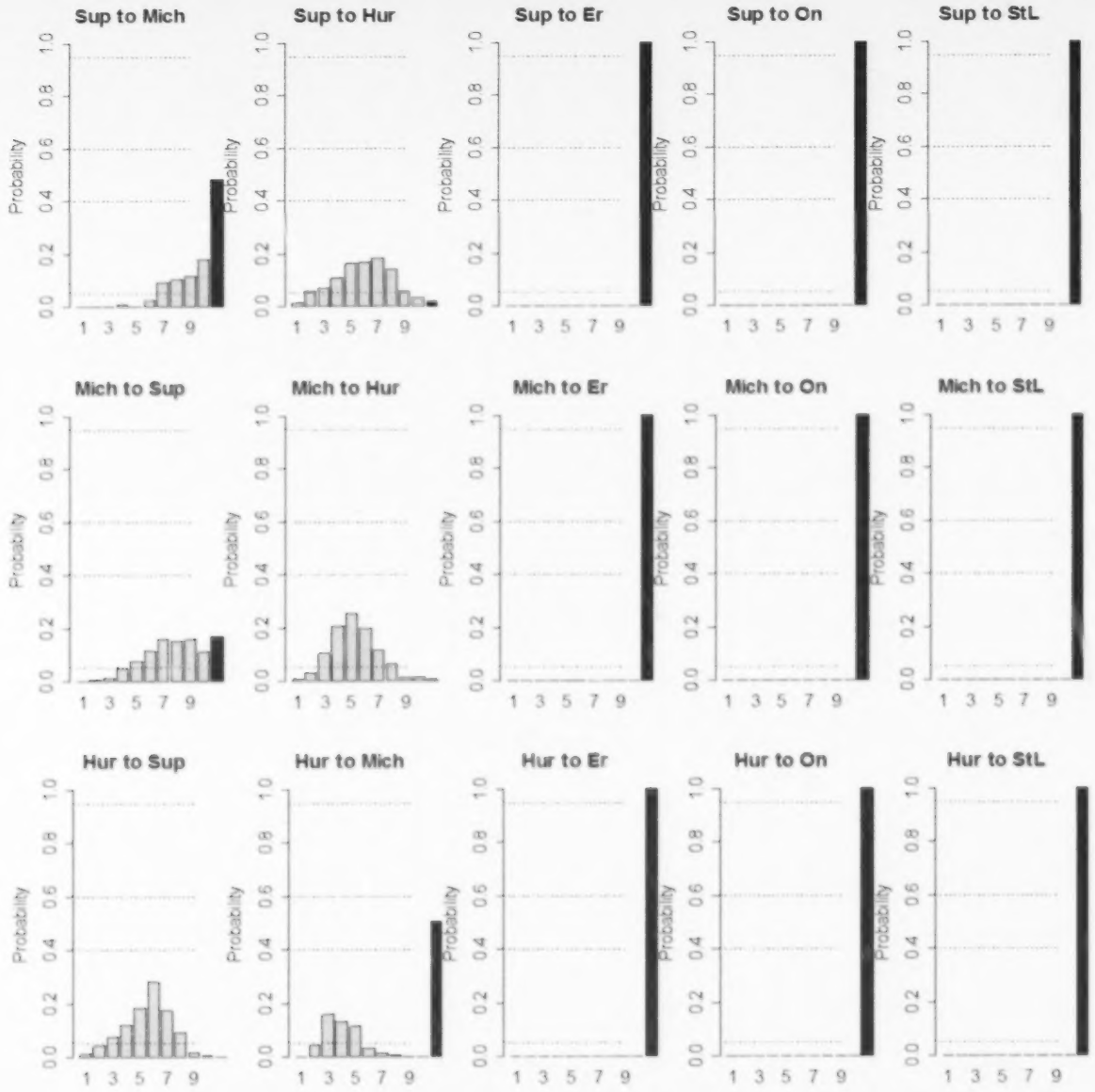

Figure A3-4. Timelines of secondary spread due to recreational boating for the non-parthenogenetic zooplankton functional group (moderate invasiveness). ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

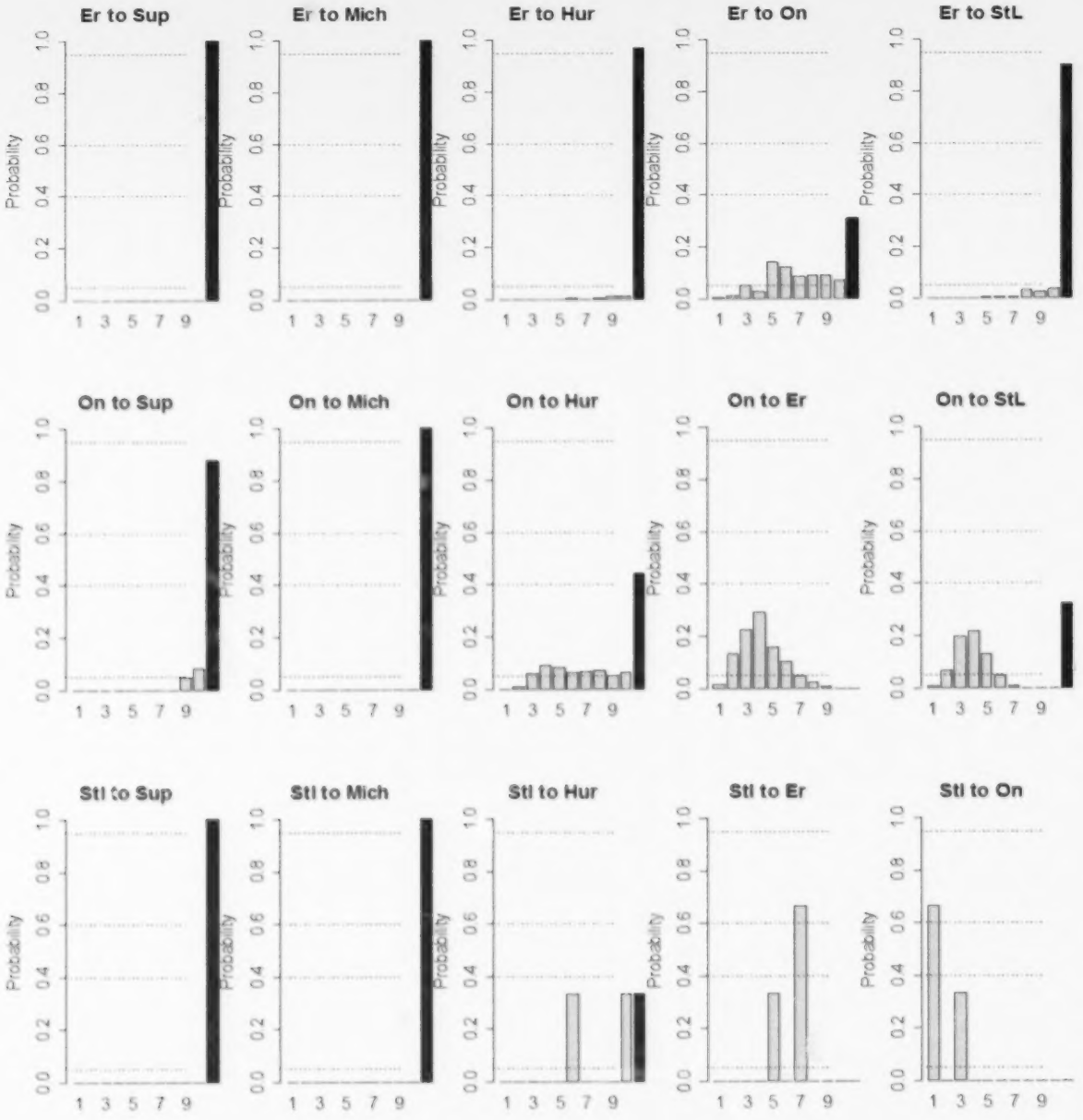

Figure A3-4. Continued.

MOLLUSC FUNCTIONAL GROUP (HIGH INVASIVENESS)

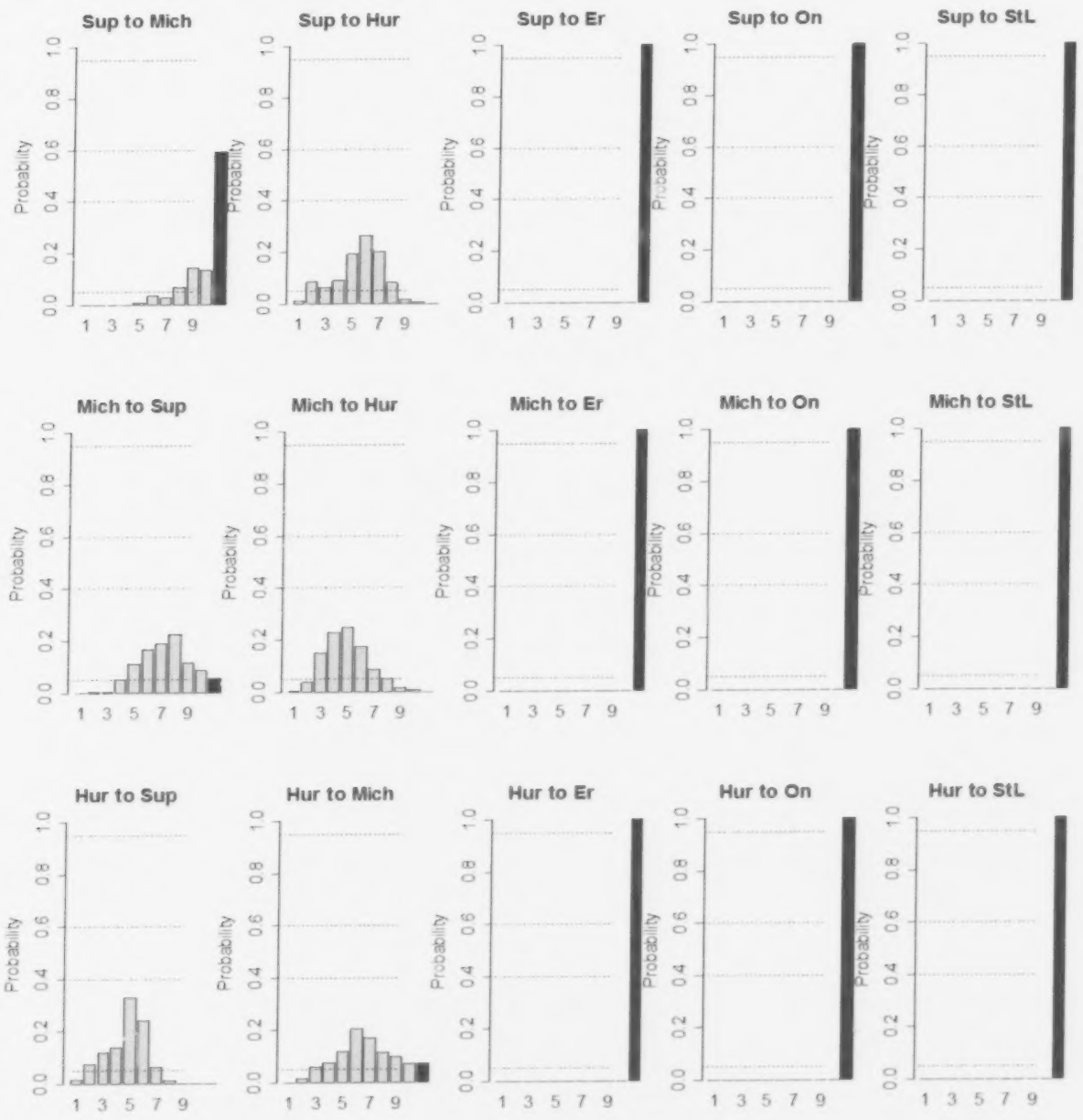

Figure A3-5. Timelines of secondary spread due to recreational boating for the mollusc functional group (high invasiveness). ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

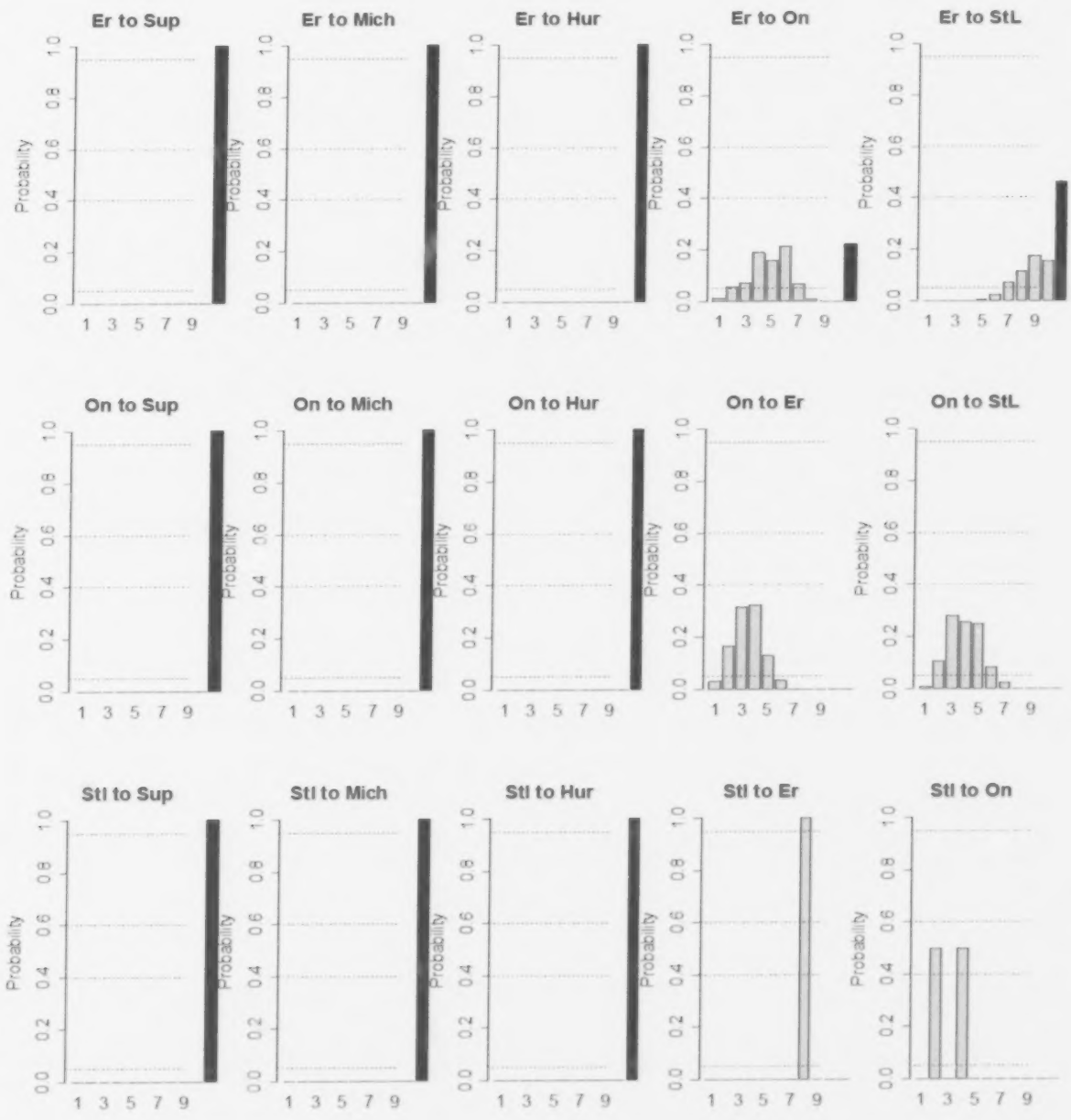

Figure A3-5. Continued.

MOLLUSC FUNCTIONAL GROUP (MODERATE INVASIVENESS)

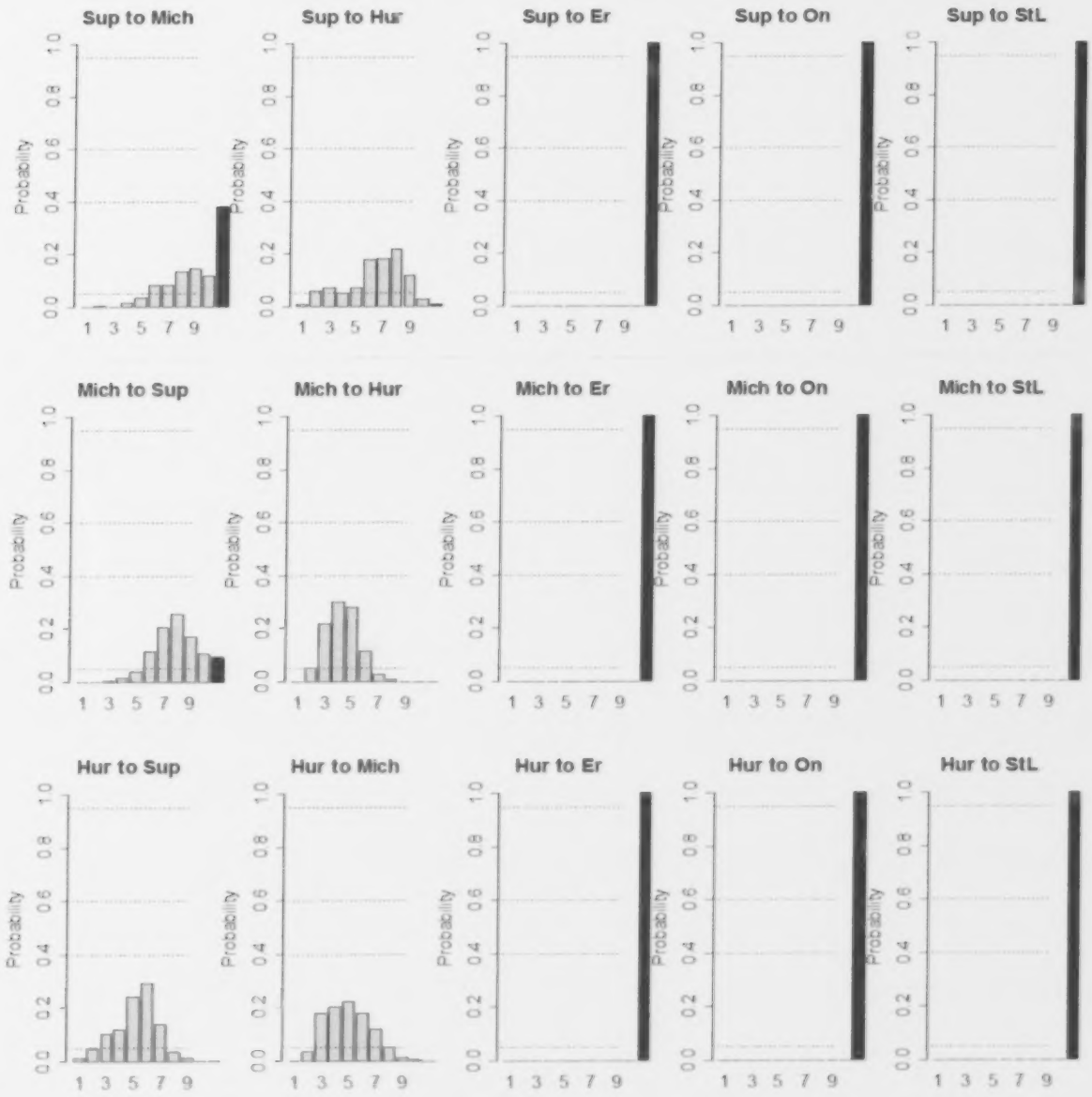

Figure A3-6. Timelines of secondary spread due to recreational boating for the mollusc functional group (moderate invasiveness). ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

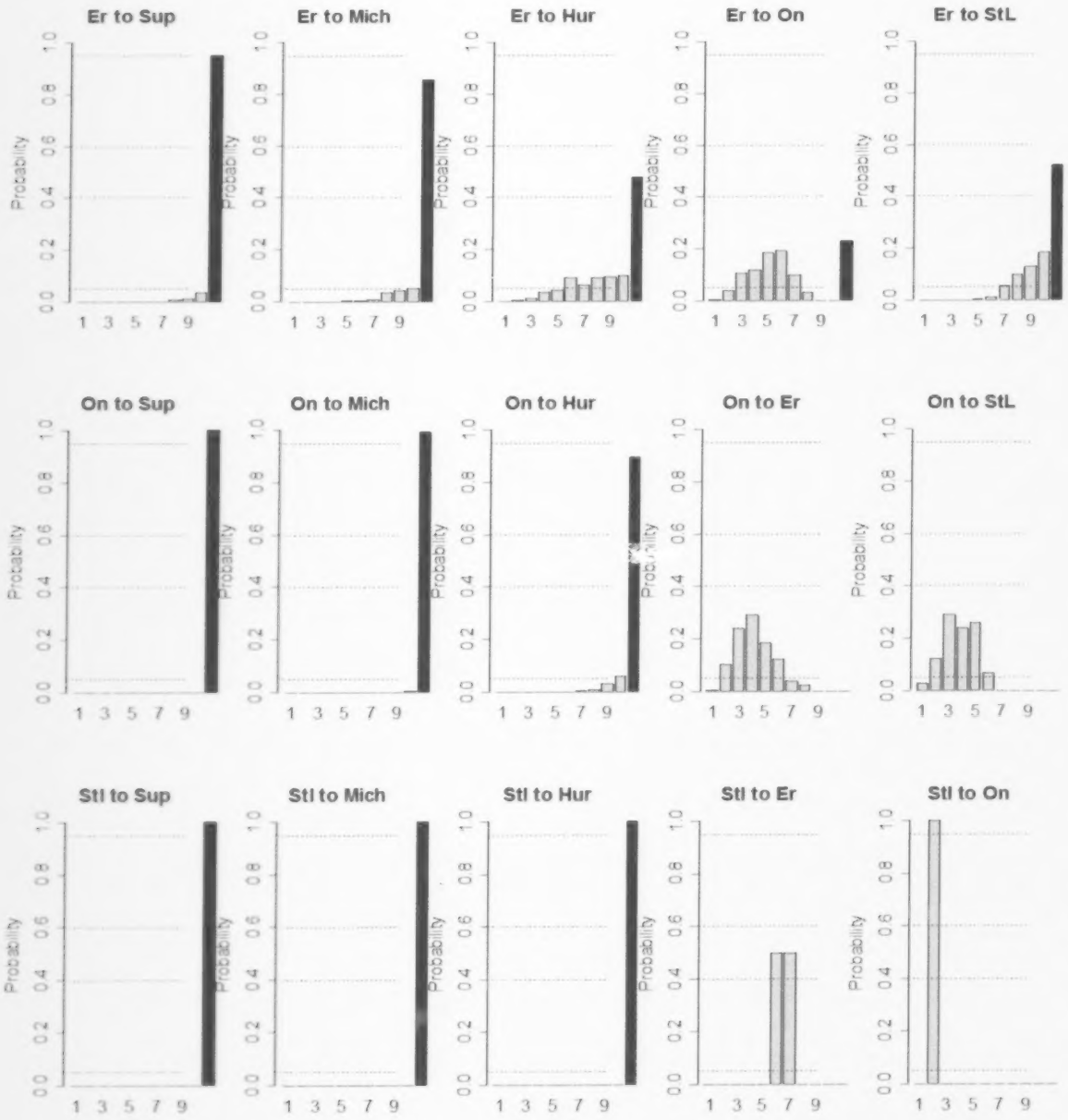

Figure A3-6. Continued.

MACROPHYTE FUNCTIONAL GROUP

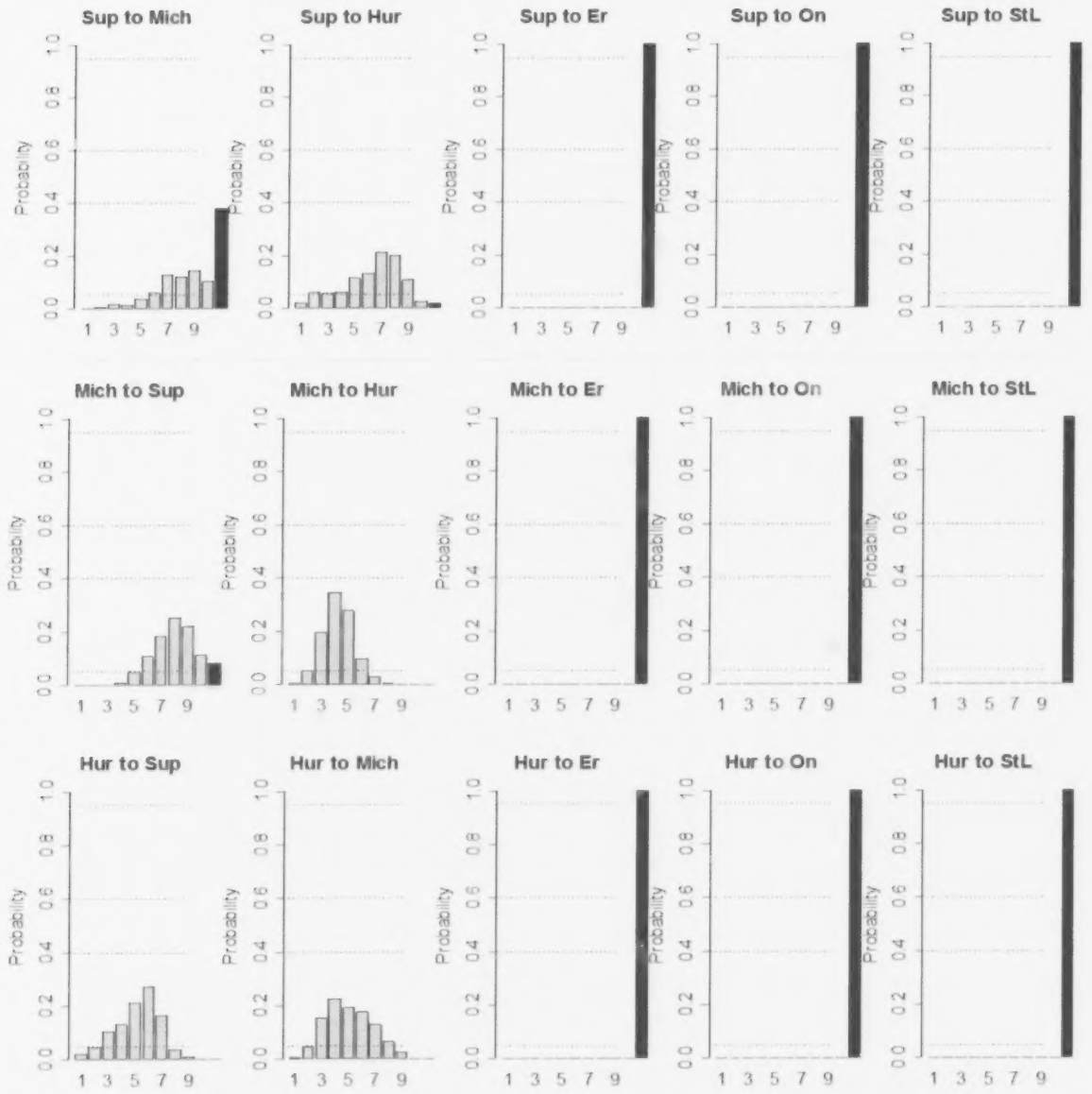

Figure A3-7.Timelines of secondary spread due to recreational boating for the macrophyte functional group (moderate invasiveness). ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

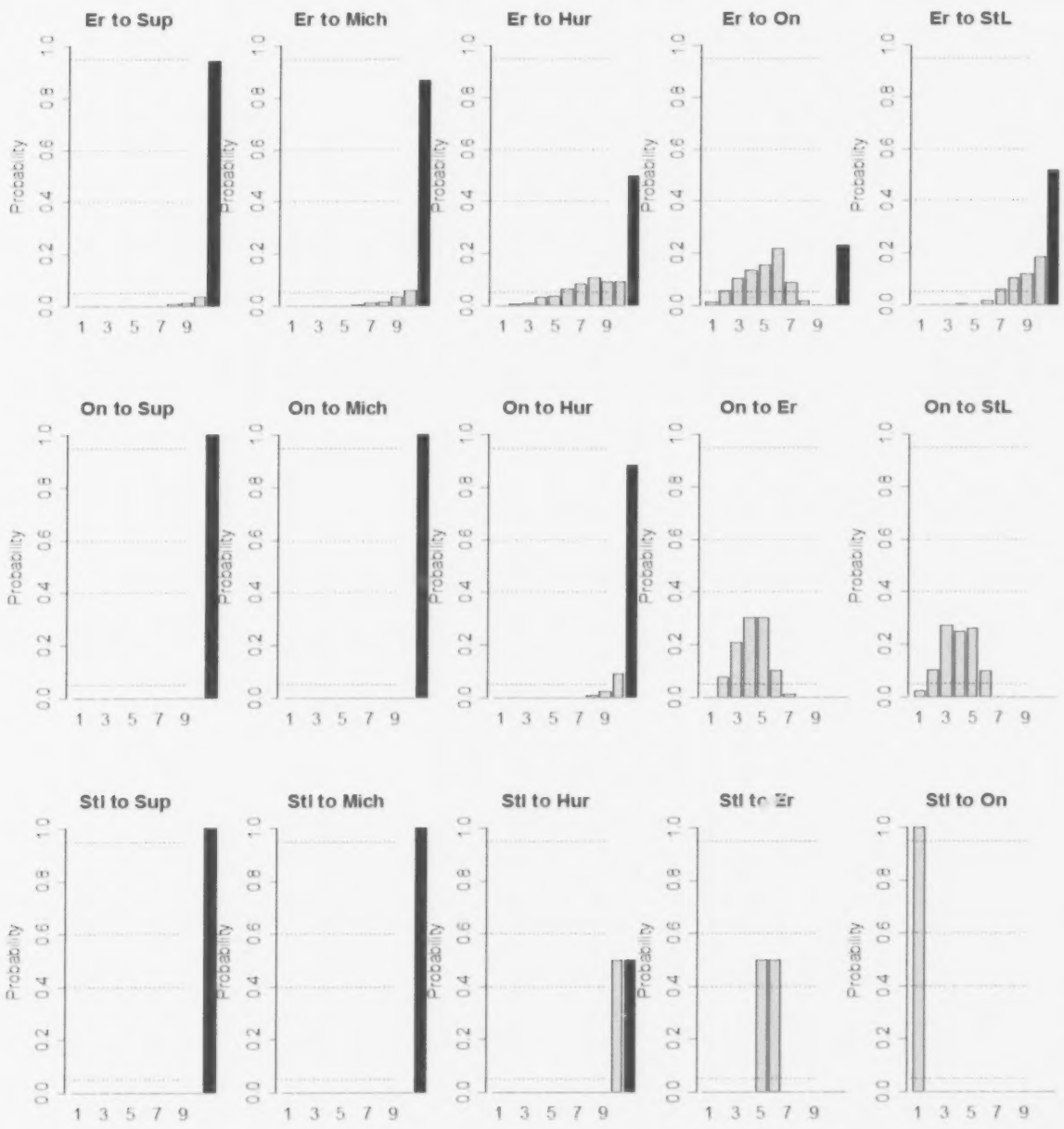

Figure A3-7. Continued.

NON-PARTHENOGENETIC ZOOPLANKTON FUNCTIONAL GROUP (HIGH INVASIVENESS) FOLLOWING A 25% REDUCTION IN MODEL PARAMETERS

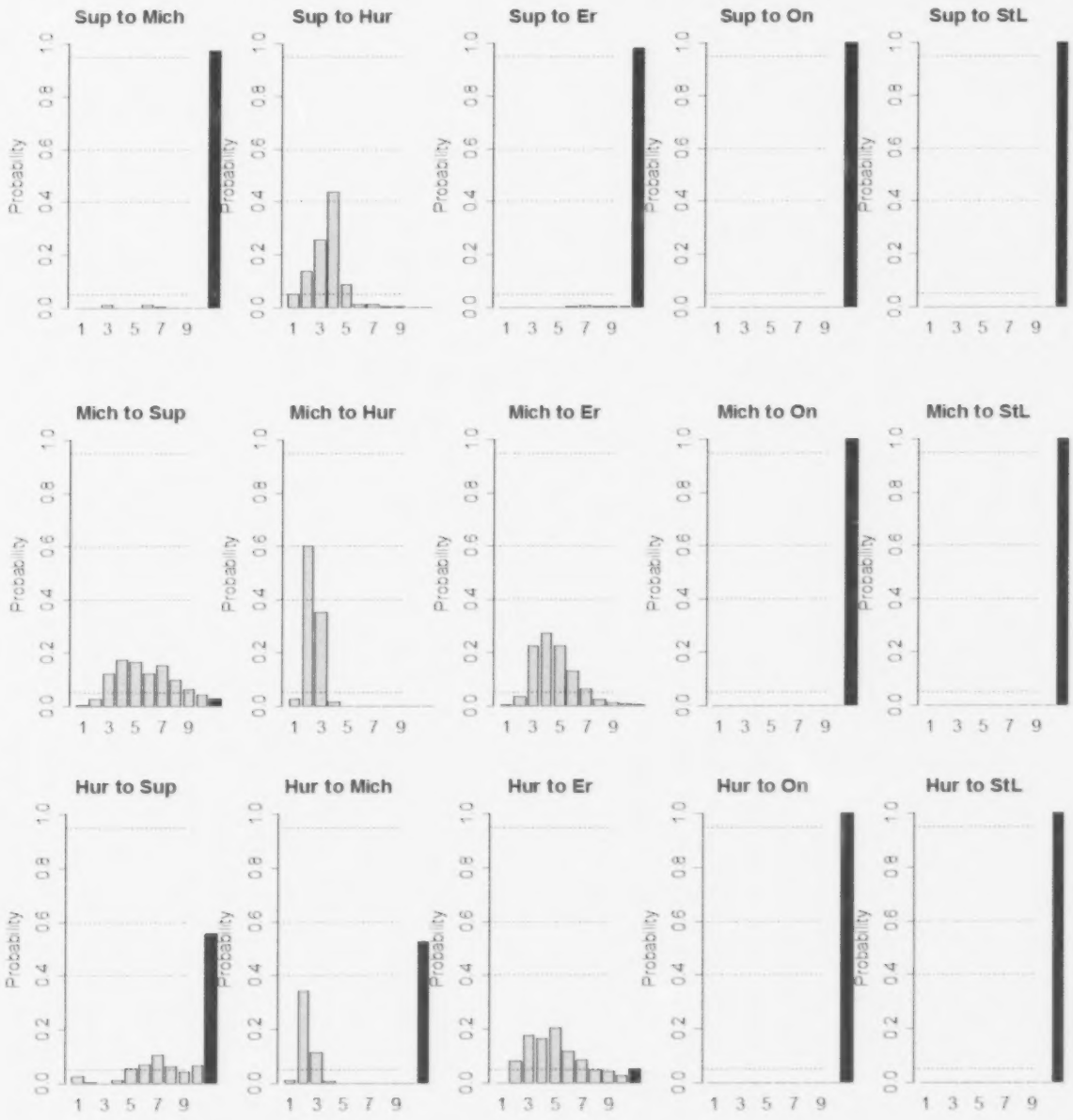

Figure A3-8. Timelines of secondary spread due to recreational boating for the non-parthenogenetic zooplankton functional group (high invasiveness) following a 25% reduction in model parameters. ***The x-axes measures spread timeline in years.*** *Black vertical bars represent a value of 11 of more years, signifying the failure of spread to occur within the ten year model period. Grey vertical bars represent spread occurring between pairs of lakes over a 1 to 10 year period.*

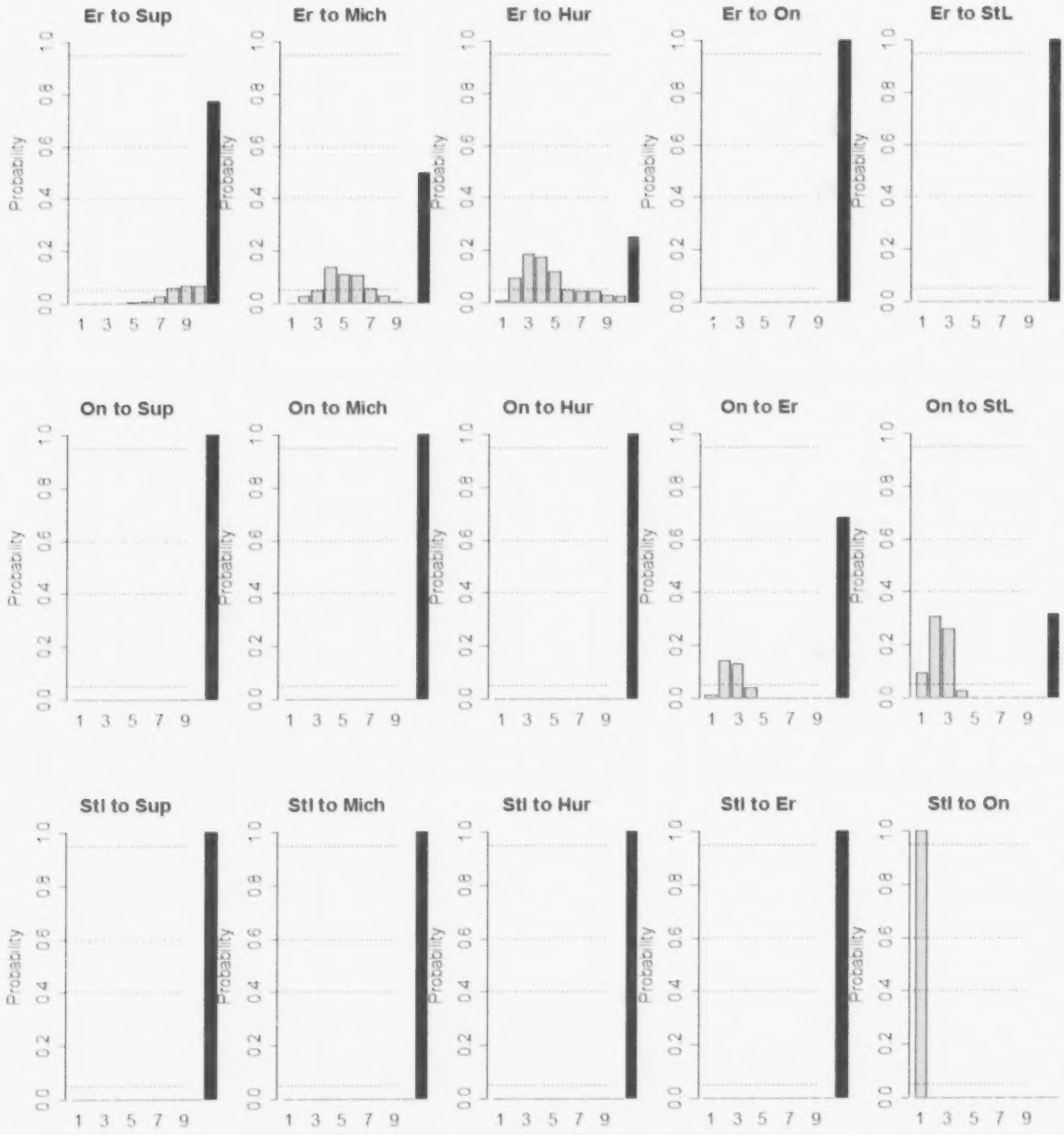

Figure A3-8. Continued.